ISSN 0007-1595

Bulletin of the
British Ornithologists' Club

Centenary volume

AVIAN SYSTEMATICS AND TAXONOMY

Edited by
Dr J. F. MONK

Volume 112A

October 1992

SHOUT
SHARE
IT

TOS. 102

AVIAN SYSTEMATICS AND TAXONOMY
—K

BRITISH MUSEUM
(NATURAL HISTORY)
30 NOV 1992
PRESENTED
TRING LIBRARY

PURCH
BRN 103046
AN 294015

PREFACE

A jubilee is a time for congratulation and a time to look back as well as forward. Having attended my first dinner of the BOC 62 years ago, and having read the *Bulletin* even earlier than that, it gave me great pleasure to accept the invitation to say a few words as introduction to this centenary issue.

The BOC was founded in October 1892, to provide an opportunity to the members of the BOU "for meeting more frequently than the customary once a year". That there was a real need for the new organisation is documented by the fact that 84 members joined the Club in the first year and that all meetings were well attended. The early meetings were devoted almost exclusively to the showing of skins of new or rare birds or of plumage aberrations. The mood of the period is well-reflected by Bowdler Sharpe's singling out a special event in the history of the young club—"The exhibition of two unrecorded eggs of the Great Auk is sufficient to endow the proceedings of the Club for 1893–94 with more than ordinary interest." Indeed, the demonstration of eggs was a regular feature of the meetings. Most of the members had their own skin or egg collections and were intensely interested in new species and in having the opportunity to see rarities. Occasionally there were informative lectures such as one by Edward Degen on the evolution of the bird's wing, published as Volume 2 of the *Bulletin*.

Forty years on, when I was able to attend some BOC dinners, they were yet memorable occasions. What a galaxy of stars attended them: Lord Rothschild, E. Hartert, W. L. Sclater, Ticehurst, Whistler, Meinertzhagen, Admiral Lynes, Stuart Baker, Gregory Mathews, Kinnear, Rev. Jourdain and many others. They all knew each other intimately and all enjoyed the festive spirit of the occasion. Of course, there was also some friendly bantering, and, among the egg collectors, there may have even been some who would not speak to each other. Rev. Jourdain was not at all amused when Col. Meinertzhagen sitting next to him handed him the box of cigars (with a few cigars left in it) saying, "And you take the whole clutch, as you are wont to do".

Even more important than this cementing of friendship was the establishing of the *Bulletin* by the Club. From the beginning it had a special niche in the ornithololgical literature, as a means for the rapid publication of ornithological novelties. In the first volume, 25 new genera were proposed and 54 new species were described. Sharpe, who was the editor of the *Bulletin*, was a strong believer in binomial nomenclature. "I cannot get three names on a label", he is said to have once said. As a result, in Volume 1 only one new bird was described as a subspecies, while 54 others were named species. I analysed these names and found that 11 were actually good new species, 28 are now considered subspecies and 15 were synonyms. The novelties presented at the Club included such spectacular things as 2 new species of albatross and numerous examples of the marvellous discoveries of endemic Hawaiian species and genera.

The spirit of ornithology has changed in the last 100 years, and the *Bulletin* has greatly enhanced its original usefulness. This is perhaps best documented by the fact that its membership has grown from 84 to some 620 with more than 230 of them living overseas. Indeed, the *Bulletin* is a truly international publication. With the *Ibis* having more and more shifted to ecological, behavioural, physiological and evolutionary papers—the same being true for the major ornithological journals in the USA, Germany and other countries—there is a real need for a journal publishing short papers on questions of taxonomy at the subspecies and species level, on significant range extensions, on aspects of the history of taxonomy, and similar subjects. The *Bulletin* is filling this important niche quite admirably.

It is rarely mentioned these days that Darwin's findings and conclusions in the *Origin of Species* were largely based on taxonomic studies. It is usually also ignored that the major contributions to the evolutionary synthesis in the 1930s–40s, made by Th. Dobzhansky, G. G. Simpson, E. Mayr and B. Rensch, was largely the result of taxonomic reasearch. Nor is it realized by those of our contemporaries who work strictly on the gene-molecular level that their own findings are quite meaningless unless placed onto the framework of good systematics. For these reasons I am firmly convinced that even today taxonomy is not a backwater, but an important branch of biological science. Whenever we do comparative researches in biology, a comparison makes sense only when based on a sound classification.

The new sphere of interest of the *Bulletin* is excellently reflected in this centenary issue, which deals with an admirable diversity of subjects. The emphasis has remained on taxonomy, but it reflects a new systematics in being, a far cry from the typological approach of the founders. Special attention is now paid to the ecological and behavioural interactions of species, to the analysis of the status of isolated populations, to the consideration of bioacoustics, and even to a survey of the new molecular methods which have already contributed so much to our understanding of the relationship of avian species, genera and families. There is no doubt the contents of the *Bulletin* are right at the frontier of modern ornithological research.

The youthful vigour displayed by the *Bulletin* guarantees many more years, may I say centuries, of useful contributions to the advance of ornithological science. My best wishes and warmest congratulations.

June 1992 ERNST MAYR

Museum of Comparative Zoology,
Harvard University,
Cambridge,
Massachusetts, U.S.A.

Status and future activities of the Standing Committee on Ornithological Nomenclature of the International Ornithological Committee (IOC)

BRITISH MUSEUM
(NATURAL HISTORY)
30 NOV 1992
PRESENTED
TRING LIBRARY

by Walter J. Bock[1]

Received 9 August 1991

Introduction

Central to the work of all ornithologists is a set of universal and stable names for the organisms they study. This problem is well known and appreciated by those committees[2] currently developing lists of vernacular names for birds, be these names, English, German, French or Spanish. Biologists have long recognized the importance of a universal, stable set of scientific names for organisms and in the early years of the 19th century had begun development of procedures and codes regulating the acceptance and use of these names. This was not an easy task and several different sets of rules, such as the Strickland and the American Ornithologists' Union Codes, gradually developed and were used by diverse groups of zoologists during the 19th century. Important procedural changes occurred during this period, such as the date to accept for the start of zoological nomenclature, different workers accepting differing starting dates. Some workers accepted pre-Linnaean names, and others used the 1st edition of Linneaus as the beginning of zoological nomenclature. Most workers during the first half of the 19th century accepted the 12th edition of Linnaeus (1766) as the beginning of zoological nomenclature, but gradually during the second half of the 1800s, the 10th edition of Linnaeus (1758) became widely accepted, and by the end of the century was used by almost all zoologists as the onset of zoological nomenclature. These diverse concepts and practices of nomenclature, involving rules of priority, led to major instability and lack of universality in scientific names for animals. Indeed many of the most muddled nomenclature problems in birds resulted from these different nomenclatural procedures, not from the discovery of previously unknown names. In 1890, the International Congress of Zoology, the only truly international group representing all zoologists, established an International Commission on Zoological Nomenclature (ICZN) and charged this body with formulating a code of nomenclature acceptable to all zoologists; but not until 1902 was a unified code of zoological nomenclature adopted by the International Congress of Zoology (ICZN 1902). It was edited and published as "*Règles Internationales de la Nomenclature Zoologique*" in 1905 (Blanchard 1905). These Règles were amended many times up to 1930, but not thereafter, and had become seriously out-of-date by the time of the 1948 Paris zoological congress. Hence, the ICZN decided that a complete revision of the Règles was needed. A full 20 years were devoted to this revision which was finally adopted by the 15th International Congress of Zoology, London, 1958 and, after extensive editing, was published as the '*International Code of Zoological Nomenclature*" (ICZN 1961), which exists today in the 3rd edition (ICZN 1985) and is generally called by zoologists interested in zoological nomenclature the 'Code'.

---

[1] Chairman, SCON; Member, International Commission on Zoological Nomenclature; Secretary, International Ornithological Committee.

[2] At the International Ornithological Congress in New Zealand at Christchurch in 1990, the IOC established 2 standing committees to work on world lists of vernacular names of birds. One committee under the chair of Burt Monroe, Jr. will work on a list of English names for birds and the other under the chair of Henri Ouellet will work on French names. Any group of international ornithologists interested in establishing a similar subcommittee to work on world lists of names of birds in other languages should contact the author.

Although these codes have served admirably to regulate the acceptance and use of scientific names, many problems both general and particular still exist. Among these is the fact that ornithologists need to know several names for most species, genera and families of birds if they are searching the literature for information on a particular taxon. For example, if one is interested in finding information on the Barn Owl *Tyto alba* in the 19th century literature, one must remember to look under the name *Strix*, by which this bird was known for most of the 1800s as well as *Hybris* and *Aluco*. The family-group name Strigidae was applied to all owls or, if subgroups were recognized, to the barn owls for most of the last century. The generic name *Procellaria* and the family-group name Procellariidae was applied to either the storm-petrels or to the shearwaters for much of the 19th century, depending who was the author. The generic name *Colymbus* Linneaus, 1758 and the family-group name Colymbidae represented an especially recalcitrant nomenclatural problem. European workers applied these names to the divers or loons, while North American ornithologists used them for the grebes, the difference in use depending on interpretation of unclear taxonomic and nomenclatural decisions made by Brisson in 1760. This problem was analysed in great detail by Salomonsen (1951) at the 1948 International Ornithological Congress, Helsinki, 1948, his paper leading to an application to the ICZN for a plenary decision. This resulted in *Colymbus* being suppressed and the names *Gavia* for the divers and *Podiceps* for the grebes being conserved along with the associated family-group names. But more importantly, Salomonsen's presentation to the 10th ornithological congress resulted in the formation of the Standing Committee on Ornithological Nomenclature (SCON).

Standing Committee on Ornithological Nomenclature

The first SCON was elected by members of the 10th International Ornithological Congress attending a special meeting arranged after the presentation of Professor Salomonsen's paper (Proc. Xth Internat. Ornith. Cong. 154). The original members were J. Berlioz (France), R. Meinertzhagen (UK), E. Stresemann (Germany) and J. Zimmer (USA) under the chairmanship of Richard Meinertzhagen. The first detailed report of this committee was presented by Salomonsen at the 12th congress (Salomonsen 1960); but the committee had been most active from its earliest beginnings.

The SCON functions under the authority of the International Ornithological Committee (IOC), the international body of ornithologists responsible for the International Ornithological Congresses. As with other standing committees acting under the IOC, the members of the SCON from the first have been appointed every 4 years shortly after the close of an ornithological congress by the new president. Appointments are made on the basis of the recommendation of the chairman of the previous SCON, which is formulated by discussion among the members of the committee. Dr. Eugene Eisenmann (American Museum of Natural History) served on this committee for many years including as its chairman, a position he held at the time of his death in October 1981. When informed in December 1981 of Dr. Eisenmann's death, Professor L. von Haartman, President of the 18th ornithological congress, appointed W. J. B. to this committee and asked if he would serve as its chairman. He has served in that capacity until the present time. Currently the SCON is composed of 14 members, as follows: Walter J. Bock, *Chairman* (USA), Murray D. Bruce (Australia), David Holyoak (UK), Ernst Mayr (USA), Gerlof F. Mees (The Netherlands), Burt Monroe, Jr. (USA), Hiroyuki Morioka (Japan), Henri Ouellet (Canada), D. Stefan Peters (Germany), Richard Schodde (Australia), L. S. Stepanyan (USSR), Karel H. Voous (The Netherlands), David Wells (Federation of Malaysia), and Hans E. Wolters (Germany) [†December 1991].

The SCON serves as an advisory body on matters of avian nomenclature. In this capacity, it holds open meetings at ornithological congresses to discuss current nomenclatural problems including pending applications before ICZN, to reach decisions on these matters and to chart its actions for the next 4 years. These meetings are open to all members of the congress, who are encouraged to take full part in the deliberations. Between congresses, the SCON remains active, dealing with nomenclatural problems as they develop and, when necessary, writing applications for submission to the ICZN and comments on pending applications.

The SCON also serves as an information source for avian biologists on all matters of ornithological nomenclature, including interpretation of the Code, assisting in the analysis of particular nomenclatural problems and helping in the writing of applications to the ICZN. *The SCON is most anxious to interact with individual ornithologists and with national check-list committees, and would appreciate being informed of all nomenclatural problems being considered by individuals and national committees.* Unfortunately this interaction is at a far lower level than the SCON would prefer. All ornithologists and all national check-list committees are urged to inform the SCON, either the Chairman directly or any member, of all questions on ornithological nomenclature being discussed. Greater interaction between the SCON and the ornithologists would result in better nomenclatural decisions and more stable scientific names for birds.

Through the Specialist Subcommittee on Ornithological Nomenclature the SCON also serves as an advisory body to the ICZN on matters of avian nomenclature. It reviews all applications published in the

Bulletin of Zoological Nomenclature and submits its recommendations and opinions to the ICZN. Although the SCON has pressed for a greater role as a Specialist Subcommittee since 1982 and although the ICZN is strongly in favour of the development of these specialist advisory groups, the Secretariat of the ICZN has shown considerable reluctance to use such specialist advisory groups. However, the SCON believes strongly the Specialist Subcommittees are in a better position than the ICZN to deal with nomenclatural matters restricted to particular groups of animals. The SCON will continue to develop its role as a Specialist Subcommittee under the ICZN.

The Secretariat of the ICZN (c/o International Commission Zoological Nomenclature, The Natural History Museum, Cromwell Road, London, SW7 5BD, U.K.; Dr. Philip K.Tubbs, Executive Secretary and Editor, *Bulletin of Zoological Nomenclature*) serves as the administrative body of the Commission. All inquiries about the work of the Commission, applications to the ICZN, questions about nomenclatural problems, orders for publications of the Commission should be addressed to the Secretariat. Inquiries about ornithological nomenclature can also be addressed directly to the SCON. The Secretariat, ICZN publish quarterly the *Bulletin of Zoological Nomenclature*, now in its 48th volume. All applications to the ICZN, comments on these applications, decisions by the ICZN and discussions about zoological nomenclature appear in their Bulletin. In addition, the International Code of Zoological Nomenclature (1985, 3rd edition; £19.00 or $35.00), the Official Lists and Indexes of Names and Works in Zoology (1987; £60.00 or $110.00) and its supplements may be ordered from the Secretariat.

Family-group names

With the publication of the new Code, family-group names were subjected to considerably greater regulation, including extending priority to these names. Unfortunately the new Code did not contain a clear *stare decisis* (= "grandfather") clause, and many workers chose to overlook its finer details. The changes to the rules of nomenclature were made with little analysis of their effect on existing and often well-established family-group names, but, and it must be emphasized, these changes in the new Code (ICZN 1961) affecting family-group names are far more complex than the simple extension of priority to these names. The Code is quite clear that the application of priority to family-group names was *not* to be used to upset established names, and it should be noted that it clearly states that names for taxa above the family-level are not covered by the rules of zoological nomenclature. With high probability, the Code will not be extended to names for these higher level taxa.

Beginning with the 1962 congress in Ithaca, NY, the SCON expressed its concern on the effects of the extension of priority in the new rules on many well-established family-group names of birds which did not possess priority. Several unsuccessful attempts were made to declare a list of well-established family-group names for the Oscines (see Salomonsen 1960: 38–39), but such broad-based applications were never accepted by the Secretariat of the ICZN. A few individual family-group names, such as

Thraupinae, Cardinalinae and Drepanididae, were conserved. However, nothing further was done for 20 years because of the daunting prospects of searching out all the avian family-group names in the old literature.

At the meeting of the SCON during the 1982 ornithological congress, Moscow, the decision was reached that the SCON would take proper action to resolve the problem of avian family-group names (Bock 1985). I undertook the task to research the history of these names and to prepare a list of family-group names published for avian families using the standard classification in Peters' *Check-list of Birds of the World*. A draft of this list of names was presented at the 1986 congress, Ottawa, where the SCON voted to complete this project and to publish the list of avian family-group names of Recent birds (Bock 1989). A final draft (Bock, in prep) was circulated to members of the SCON and other interested ornithologists just prior to the 1990 congress, Christchurch, and this list and future action by the SCON were discussed at the open meeting there. Copies of this final draft are available to interested ornithologists by writing to me. Over 1200 family-group names are available for Recent birds (i.e. those covered in Peters' Check-list); the list does not include names for families of fossil birds. After this list is published, an application will be made to the ICZN, requesting that this list of avian family-group names be declared as the base-line for all future nomenclatural decisions of avian family-group names for Recent birds. The names on this list, with their authors and dates of publication, by such declaration will be fixed; and names not on this list will be declared not available for purposes of zoological nomenclature for Recent birds. These actions are in line with the current thinking of the ICZN, which is to encourage the development of lists of available names for groups of animals, and to fix these lists as the only names available for each group.

Generic names

Following discussion of the list of family-group names, the SCON considered the general concept advocated by the ICZN to develop lists of available names for groups of animals. The group approved of this approach and proposed a resolution for consideration by the IOC at its meeting. This resolution which was approved by the IOC reads as follows:

> 'WHEREAS the International Commission on Zoological Nomenclature has the difficult central role in insuring maximum ease of communication between zoologists by insuring the stability and universality of names for the diverse organisms studied by the zoologists,
> THEREFORE BE IT RESOLVED that the International Ornithological Committee at its meetings during the XX International Ornithological Congress, Christchurch, New Zealand, 2–9 December 1990 congratulates and supports the International Commission on Zoological Nomenclature in its efforts to increase continuity of zoological nomenclature by the conservation and stabilization of established names and directs its Standing Committee on Ornithological Nomenclature to assist the International Commission on Zoological Nomenclature in these efforts.
> MOREOVER, the International Ornithological Committee recognizes and congratulates the pioneering actions of the Standing Committee on Ornithological Nomenclature in developing a list of available family-group names of birds and urges this committee to undertake similar projects on genus-group and species-group names of birds.'

In connection with this resolution, Murray Bruce said that he was developing a computer-based data bank of generic names for birds. The SCON discussed the possibility of undertaking a project of completing this list of available generic names for birds similar to that completed for family-group names, publishing it and applying to the ICZN to declare this list as the base-line for all future nomenclatural decisions on generic names for Recent birds. This project was approved and Murray Bruce and Walter Bock were directed to consider ways to complete the project after the list of family-groups names was finished.

Delays in actions taken by the ICZN

Many members of the SCON and other ornithologists have expressed serious concern about the long waits on applications submitted to the ICZN, delays arising in the work of the Secretariat. For example, the application on conserving the family-group name Threskiornithidae was submitted in 1975 and published only in 1984; but to date it has not been submitted to the membership of ICZN for their vote. The application to conserve the generic name *Cacatua* was published in 1964, with a substitute set of requests published in 1965. Although ornithologists have agreed informally to use this name, the Secretariat of the ICZN delayed a vote for apparently rather trivial reasons. After a full discussion of these and other cases, the SCON voted to urge the ICZN and its Secretariat to speed the measures by which applications are processed, published and final action taken by the ICZN. Further, the SCON urged the ICZN and its Secretariat to increase its use of the SCON as a specialist advisory committee and to submit to the SCON for its consideration all applications, upon receipt, dealing with birds. At the same time, ornithologists are strongly urged to interact with the SCON in their analysis of possible nomenclatural matters and in the development of applications for submission to the ICZN.

Because ornithologists rarely contact the SCON on nomenclatural analyses they have undertaken, and usually do not inform the SCON of their individual applications and comments submitted to the ICZN, the SCON does not and cannot have a good appreciation of the magnitude of this problem of delays. For example, we do not know of, or how many, applications on avian nomenclatural matters have been submitted to the ICZN and are still unpublished. Therefore, all ornithologists are urged to keep the SCON informed of their correspondence with the ICZN, including where possible sending copies of all applications and comments and of all correspondence with the Secretariat. The SCON would appreciate learning of any problems, including delays in publications, extensive editing of applications and comments in which real changes of meaning occurred.

Scientific names used for birds affect the work of all ornithologists, and the SCON is dedicated to the central goal of the International Code of Zoological Nomenclature, as expressed clearly in its Preamble, namely the maximum stability and universality of these names. This goal can best be reached by full cooperation between all ornithologists. The SCON appreciates the offer of the British Ornithologists' Club to present this report of its recent activities and we hope that its publication will encourage ornithologists worldwide to interact more with the Standing Committee on Ornithological Nomenclature and its work.

References:
Blanchard, R. (Ed.). 1905. *Règles Internationales de la Nomenclature Zoologique Adoptées por la Congrés Internationaux de Zoologie*. F. R. Rudeval, Paris.
Bock, W. J. 1985. Report of the Standing Committee on Ornithological Nomenclature. *Proc. XVIIIth Internat. Ornith. Cong., Moscow, 1982*: 29–32.
— 1989. Report of the Standing Committee on Ornithological Nomenclature. *Proc. XIXth Internat. Ornith. Cong., Ottawa, 1986*: 62–68.
— 1992. Report to the XXth International Ornithological Congress from the Standing Committee on Ornithological Nomenclature. *Proc. XXth Internat. Ornith. Cong., Christchurch, 1990*: 84–86.
— In Prep. History and nomenclature of avian family-group names.
International Commission on Zoological Nomenclature (ICZN). 1902 *Rules of Zoological Nomenclature*. [English Version of the "Règles internationales de la Nomenclature zoologique."]. Pp. 963–972. *In*: 'Verhandlungen des V Internationalen Zoologen Congress zur Berlin. 12–16 August 1901'. P. Matschie, Ed. G. Fischer, Jena.
— 1961. *International Code of Zoological Nomenclature, adopted by the XV International Congress of Zoology*. Internat. Trust Zool. Nom., London: xviii + 176 pp.
— 1985. *International Code of Zoological Nomenclature, adopted by the XX General Assembly of the International Union of Biological Sciences*. Third Edition. Internat. Trust Zool. Nom., in association with the British Museum of Natural History, London and the University of California Press, Berkeley and Los Angeles: xx + 338 pp.
Salomonsen, F. 1951. A nomenclatural controversy: The genus *Colymbus* Linnaeus 1758. *Proc. Xth Internat. Ornith. Cong., Uppsala*: 149–154.
— 1960. Report of the Standing Committee on Ornithological Nomenclature. *Proc. XIIth Internat. Ornith. Cong., Helsinki*: pp. 30–43.

Address: Dr. Walter J. Bock, Dept. of Biological Sciences, Columbia University, New York, NY 10027, USA

© British Ornithologists' Club 1992

Taxonomy of lower categories—suggested guidelines

by Dean Amadon & Lester L. Short

Received 7 January 1992

Introduction

In the 1940s came a wider realization that evolution provides the theme for all aspects of biology. One of the pillars of this synthesis was a "biological" species concept, sponsored then and later by Mayr (1942, 1963), among others. Reduced to essentials, a species is a self-contained, interbreeding, interfertile population. Each such reproductively isolated species is forever on its own—to evolve, to adapt, or to face extinction. Such species, and the individuals comprising them, constitute the diversity and richness of life on earth. Recently this species concept has come under scrutiny and some opposition. On the one hand the virtual explosion of new laboratory techniques, here subsumed under the rubric "molecular biology", has permitted penetrating analyses of populations. In another direction, more rigorous cladistic methods of phylogenetic analysis, associated in part with the work of Hennig (1966), pose new questions.

Several other species concepts have been proposed in recent years. Meanwhile the scientific community and the public at large continue to rely on the prevailing understanding of this taxon. The biochemist seeking a vaccination for malaria assumes that he has been correctly informed by the taxonomist that the mosquitoes before him are the vector of a particular strain of malaria. The conservationist assumes that the species he is seeking to preserve are realities.

We briefly review some conflicting species concepts and conclude that, while they shed new information on the complex and variable evolutionary process of speciation, they pose no threat to the belief, may one call it a fact, that the vast majority of living organisms are (or for fossils, *were*) organized into the self-contained interbreeding units, which Noah, loading his Ark, called species. Our main purpose is to present an ordered scheme of categories dealing with taxa at or near the species level. As we make clear below, one is obliged in consideration of taxa at any given level, to treat matters to the next higher level (here, the genus) and to the next lower level(s), subspecies and even demes. Others have initiated this process, piecemeal, as indeed have we (see References). A few new terms are defined as necessary to complete the framework.

The working taxonomist is faced with various problems. New terminology is rife; we attempt to separate what is useful from what is superfluous or impractical. Taking it for granted that since the time of Darwin classifications should embody as much as possible of known or presumed phylogeny, to what extent can the veritable flood of information and theory from molecular biology and cladistics be incorporated into a classification, and what part left to cladograms or other means of presentation? Must not a classification also reflect degree of change; after all to evolve is to change over time. If on some planet the only result of 3 or 4 billions of years of evolution were 200 or 300 nearly identical species of "seaweeds", how significant would a cladistic analysis of their phylogenies be? Linnaeus, a century before Darwin, set up his higher categories because he realized that, for example, seals are less closely related to cats than is one genus of cat to another. Several of the definitions refer to monophyly. Some groups have so many traits in common, that monophyly can scarcely be questioned; e.g. the living species of flamingoes (Phoenicopteridae). Often however, especially when based on fossil specimens, few and imperfect, monophyly is a tentative conclusion. The methods and special taxonomy of cladistics are of assistance, though fossils pose major problems (Van Valen 1978). Molecular biology plays an increasing role but with rare exceptions is limited to living or recently extinct organisms.

Definitions of terms

To facilitate discussion we begin by defining the terms that we find essential or useful. The numbers correspond to those in the following analysis. Three terms, marked with an asterisk, are here introduced for the first time. Four of the terms: species, subspecies, genus, subgenus are formal designations, rules for whose usage are set forth in the Rules of the International Commissions on Nomenclature—botanical and zoological.

1—SYMPATRIC (SYMPATRY). Taxa that occur in the same area (range) at least in part and at least during the reproductive season.

2—ALLOPATRIC (ALLOPATRY). Taxa whose ranges do not overlap, at least during the reproductive season.

a—PARAPATRIC ALLOPATRY. Allopatric taxa whose ranges are (in part) contiguous, but do not overlap.

b—DISJUNCT ALLOPATRY. Allopatric taxa whose ranges are spatially separated.

3—DEME. Within a species, a localized diagnosable subpopulation of less than subspecies rank.

4—SUBSPECIES. Within a species, a named, recognized allopatric subpopulation which is (still) genetically compatible with other subpopulations, but is set apart by a concordant array of genetic and phenotypic characters.

5—MESOSUBSPECIES*. A subspecies that is not approaching species status.

6—MEGASUBSPECIES. A subspecies that is approaching species status.

7—SUBSPECIES GROUP. A monophyletic subset of subspecies within a species.

8—(SEXUAL OR GAMETIC) SPECIES. A freely interbreeding, interfertile, self-contained population (or group of subpopulations) of organisms.

9—MONOTYPIC SPECIES. A species without recognized subspecies.

10—POLYTYPIC SPECIES. A species with recognized subspecies.

11—MESOSPECIES*. A polytypic species none of whose subspecies is approaching species status.

12—MEGASPECIES. A polytypic species composed of megasubspecies. (Term introduced by Crawford-Cabral 1986.)

13—ISOSPECIES*. A species that is not a member of a contemporary superspecies, i.e., that is not an allospecies.

14—ALLOSPECIES. One of the allopatric species comprising a superspecies.

15—SIBLING SPECIES. Species so similar phenotypically that they are hard to distinguish.

16—GENUS. A named, recognized, monophyletic group of species, in rank between the species and the family (or subfamily).

17—SUBGENUS. A named, recognized, monophyletic subset of species within a genus.

18—POLYTYPIC GENUS. A genus containing more than one species.

19—MONOTYPIC GENUS. A genus containing only one species.

20—QUASI-MONOTYPIC GENUS. A genus consisting of one superspecies.

21—SPECIES GROUP. A monophyletic subset of species within a genus or a subgenus, but not formally named (as are the genus and subgenus).

22—SUPERSPECIES. A group of allopatric species (hence allospecies) deemed to have been derived from (mega)subspecies of a single antecedent species.

23—BIOGEOGRAPHICAL UNIT (formerly, BIOGEOGRAPHICAL SPECIES). A term applied to ISOSPECIES and to SUPERSPECIES considered as equivalents; that is, the allospecies of a superspecies are not listed or evaluated separately.

24—ASEXUAL POPULATION, CLONE, or "SPECIES". A population in which no interchange of genes occurs among individuals.

Discussion of terms

1, 2—SYMPATRY, ALLOPATRY

From the definitions it will be evident that we consider parapatric allopatry and disjunct allopatry as two kinds of allopatry. Thus we do not follow Prigogine (1984, 1985) who recommended parapatry as a third category equivalent to sympatry and allopatry, limiting the latter to disjunct allopatry. Some subspecies of a species may be parapatric, as on a continent, with others disjunctly distributed on surrounding islands. The same is true of the allospecies of a superspecies. Furthermore, as a result of changes in sea level, orogeny, or climate, taxa which were once parapatric may become disjunct or vice versa. Such changes may at times occur abruptly, due for example to stream capture, volcanic eruptions, or the like. The degree of geographic separation may vary from slight (patchy distribution) to great (on different continents). It seems best to subsume parapatric allopatry and disjunct allopatry under allopatry.

Parapatry infers visual and vocal contact, and thus the opportunity for physical contact between individuals of 2 taxa in the appropriate season or time of year for breeding activity (subspecies and allospecies of birds may come into sympatry seasonally, through migration, when they do not breed). Taxa are not parapatric when, for example, they involve forest animals separated by a broad river which they do not cross, and across which they cannot hear or see individuals (but at the headwaters of such a river they may become parapatric).

The important fact is whether 2 taxa overlap and hence are *ipso facto* (sympatric) species or whether they are spatially separated and thus could be either subspecies or species. Taxa that are in parapatric allopatry are more profitably studied by the evolutionist than spatially separated ones because actual contact provides a test for the completion of speciation. Nevertheless, disjunct populations are a far more fertile source of new species, because of their often greater genetic isolation, and their frequent occurrence in more distinct ecotypes.

Smith (1965) proposed the term "dichopatric" for what we have called disjunct allopatry; the term disjunct had been used for this purpose at times. Mayr (1982a,b) proposed a term "peripatric" for instances of disjunct allopatry resulting from dispersal, hence "peripatric speciation." This will usually involve a small number of individuals, and will result in the "founder effect" of Mayr (1948a; see also Carson 1989). Cracraft (1984) agreed with this and went on to suggest that Smith's term dichopatric be restricted to the other class of disjunct populations, those resulting from vicariant events such as orogeny. He noted that in some biogeographic and other analyses, it is useful to make this distinction.

Still, the terminology leaves something to be desired because dichopatric was originally proposed to apply to *all* types of disjunct allopatry, while peripatric is doubly confusing both because of its similarity to parapatric (when spoken as well as in print) and because such peripatric populations are not parapatric but disjunct. That is, it is not a kind of parapatry. Probably in those instances where it is necessary to make the distinction, it may best be simply explained which type of disjunct allopatry is meant.

3—DEME

Species, except those with very small ranges, or perhaps wide-ranging promiscuous ones (some cetaceans), tend to become subdivided into allopatric, local, often weakly characterised, subpopulations called demes. Local populations of birds that have developed song dialects are examples. Such trends may at first have little or no genetic basis, but if dispersal and gene flow are minimal and isolation continues, these demes can evolve through subspecies to species. Or, adaptive gene combinations may become established more easily in small populations like demes and can then gradually permeate the entire species.

4—SUBSPECIES

When subspecies are in parapatric allopatry they interbreed and exchange genes where their ranges meet. This will usually not lead to genetic swamping and the merger of the subspecies, for each is often adapted to a slightly different ecotype. Equally important, however, as with demes, favourable gene combinations may spread throughout the species. The amount and nature of the gene flow are affected by population structure, dispersal rates, the distribution of preferred habitats, and other factors. The access of diverse populations to beneficial genes and gene combinations is potentially of great value, and is possible because of reproductive compatability. When variation is clinal, as is often the case, it is unwise to name subspecies unless the terminal populations are strikingly unlike. The same is true of non-concordant clinal variation; e.g., size may increase northwards and paleness westwards. Such variation may, to a degree, result from non-genetic (in the immediate sense) responses to slowly changing ecotypes. Put otherwise, most populations that warrant subspecific status will represent a more or less integrated suite of characters, some adaptive, some neutral.

The use of the term "recognised" in the sense of "visibly different" in our definition of the subspecies is deliberate. The formal naming of spatial subpopulations should be restricted to those that are morphologically (phenotypically, and proven or presumed genetically) separable at some reasonable level, e.g. 90%. This is as true now as it was a half-century ago when Bullough (1942) unwisely named the resident European Starlings *Sturnus vulgaris* of Great Britain a subspecies, *britannicus*, to separate them from the phenotypically inseparable, migrant Scandinavian Starlings, which overwinter in the British Isles.

Clamour for the abolition of the subspecies as a formal category has come mostly from those unconcerned with the broad aspects of geographic variation and speciation; for defence of the subspecies see, e.g. Smith & White (1956), Amadon & Short (1976). The usefulness of traditional and formally recognized subspecies was discussed in a series of short papers by Mayr (1982d) and others. Palaeontologists might be expected to have little need for subspecies, but Simpson (1961: 176) recommended "successional" (temporal) subspecies when analyzing some fossil sequences.

Many taxa known by intergradation or reasoned by inference to be conspecific are nonetheless so distinct that taxonomists, general biologists, conservation and government agencies, and laymen seek a name for them. By providing a subspecies name this need is met; further, the unfortunate tendency to elevate such infraspecific taxa to the status of species is lessened. In better known groups most such taxa already have names available.

The simple scanning of check-lists or other publications in which subspecies are listed can provide information and suggest lines of investigation for many studies of biogeography, biodiversity, ecology and evolution, including: comparison of genetic variability with phenotypic variability; analysing why some congeneric species show more variability than others; comparison of levels of differentiation associated with degree of geographic isolation; size of range (islands); and amount of variation in migratory versus non-migratory populations. Subspecies are increasingly recognized as important in environmental conservation and the maintenance of biological diversity. Government agencies can (and should) deal with named, definable subspecies, which provide a convenient, logical and biologically significant level of categorization for maintaining biodiversity (O'Brien & Mayr 1991). Endangered status, usually given when a species is reduced to a level below 5000 individuals, ought, for purposes of preserving significant genetic diversity, to be applied also at the subspecies level. Certainly this would serve the long-term goal of preserving biodiversity, and indeed species. It also obviates the need felt and too often expressed by some conservationists, to inflate subspecies to the level of species solely to preserve them.

To be sure, too much emphasis upon subspecies when shaping public policy can occasionally be a double-edged sword. Efforts to save the gravely endangered Florida population of the cougar or "panther", *Felis concolor*, have been questioned because apparently a few individuals from Central America, which *may* represent a slightly different subspecies were at one time released in Florida, thus "tainting" the local population. But surely the important point is to save the only remaining remnant of the species in the eastern United States.

Subspecies are accepted by Avise & Ball (1990); to qualify as a subspecies they ask that a population exhibit concordant characters, preferably demonstrated molecularly, but add that sometimes a concordance of phenotypic characters will have to suffice because it is too much to expect that all populations of organisms will be analysed genetically.

For those who would argue against formal recognition of the subspecies, it may be noted that this in no way alters the conclusion that there is a fundamental difference between infraspecies populations (not genetically isolated) and species (genetically isolated). Indeed, even those who may avoid formally named subspecies, will have to use some method of categorizing and ranking geographically isolated, distinctive, but infraspecific populations.

5—MESOSUBSPECIES*

A term here proposed for the great majority of subspecies, those that are not approaching species status. Mesosubspecies may be well-defined by one or more traits, some at a level of 100% separation from one another. Several mesosubspecies may form one megasubspecies of a megaspecies, presenting problems addressed by Amadon & Short (1976). A polytypic species comprised only of mesosubspecies (that is, lacking megasubspecies), is a mesospecies as defined above. Mesosubspecies may be clustered into subspecies groups, if that is desirable.

6—MEGASUBSPECIES

In an earlier paper we (Amadon & Short 1976) introduced this term and suggested procedures for the use of parentheses to indicate them. Thus *Circus* (*cyaneus*) *hudsonius* indicates that the North American form of the Northern Harrier is judged to be a subspecies of the Eurasian *Circus cyaneus*, but one which is approaching species status. The 2 are completely isolated geographically. In more general works merely the species name, *Circus cyaneus*, would be used for both.

There are a great many such taxa, hundreds in the Class Aves alone, whose status, whether species or megasubspecies, is in part a judgmental opinion. In the harrier example, the 2 megasubspecies are not greatly different, but the genus is one with some quite similar sympatric species, which suggests caution. On the other hand a third taxon, related to the 2 just noted, *cinereus* of South America, is much more distinct and we think it is a valid species. Then *cyaneus* and *cinereus* are the two allospecies of a superspecies *Circus* [*cyaneus*]. Thus the megasubspecies provides a repository for, as the definition states, taxa that, on the available evidence, are concluded not to have crossed the species threshold, but to be approaching it. (See also number 12, megaspecies, below.)

7—SUBSPECIES GROUP

The subspecies of polytypic species often permit separation into groups with shared characteristics, frequently along geographical lines. The category is informal, so one may use it without assigning all the subspecies in a species to subspecies groups (though it is often heuristic to do so), while recognizing that a single subspecies may form its own group. In megaspecies the megasubspecies themselves essentially constitute subspecies groups and it will rarely be worthwhile to attempt further groupings.

Because of "leapfrog" or mosaic evolution, disjunct subspecies occasionally are phenotypically more similar than parapatric ones. Or, for example, dark-coloured subspecies of larks or mice may occur wherever there is a sizeable outcropping of black lava. To associate such subspecies may result in groups that are not monophyletic, requiring careful taxonomic analyses.

8—SPECIES

Characteristics. A species is an interbreeding, interfertile (i.e. Mendelian) population of organisms. We have added "self-contained" rather than "kept separate from other populations (species) by isolating mechanisms". Carson (1989) favours such a concise definition as emphasizing the *sine qua non* of the species, a common gene pool, and notes that Dobzhansky (1950), the pioneer in applying genetics to the species concept, did the same.

The species is often, even usually, defined as "a group of interbreeding populations". This is misleading. Many, perhaps most, species evolve from a small isolated population—the "founder effect" of Mayr (1982a) or the "punctuated equilibria" (in part) of Gould & Eldredge (1977) (see also Barton 1989). Some species, because they always have small ranges, remain essentially panmictic; others become so as they decline towards extinction.

Most species do eventually break up into more or less spatially segregated subpopulations. But these subpopulations, from one point of view, disrupt the species away from panmixia; when sufficiently isolated and for sufficiently long periods, they will diverge through the stages of deme, mesosubspecies, megasubspecies, species, and even genus. To define the species as based upon or requiring interbreeding *populations* is quite simply an error, but subpopulations must be mentioned to make it clear that these usually arise and remain part of a species for indefinite periods.

Species vary over space and time and this, together with their intrinsic variability, as enhanced by sexual reproduction, open the way for the evolution of new species. It is not surprising that the species definition sometimes has to be qualified to cover specific cases, of which the 3 following are among the more significant.

(a)—As already noted, species, especially widely distributed ones, tend to break up into subpopulations. These may be in either parapatric or disjunct allopatry; some of the latter may be only "potentially" capable of interbreeding with other subpopulations, e.g. rats, *Rattus*, stranded on an island. Others, of course, are permanently stranded, as by the submergence of the Siberian-Alaskan Landbridge, yet such populations may remain conspecific for long periods.

(b)—Closely allied species (allospecies), sometimes continue to interbreed (hybridize) to a limited extent; an extent insufficient to undermine their genetic integrity (see later discussion).

(c)—Over geological time, fossil lineages must be arbitrarily broken up by the taxonomist into species, genera and families, keeping them as equivalent as possible to ones based on contemporary taxa. As Simpson noted (1961: 165), any species, living or fossil, e.g. *Homo sapiens*, could in theory be traced back generation by generation to a one-celled ancestor; but to designate such an entire lineage as a single species is "not only useless but somehow wrong in principle. Certainly the lineage must be chopped into segments (species, genera, families) for the purpose of classification and this must be done arbitrarily". Gaps in the fossil record, doubts as to exact lineage, and other factors make the process of subdividing such lineages less difficult than might be expected.

Bock (1986: 38) disagrees and concludes that species have no beginning and no end (except extinction). But if a species occurs in a Palaeocene fossil bed, for example, and a taxon in the same lineage in another deposit from the Eocene 15 million years later, but by now much changed, is there any recourse but to name it as new? To continue to use the name applied to a quite different earlier stage would be completely confusing.

Some cladists have tried to circumvent the problem of lineages over secular times by positing that every time a species buds off a new one, the parent species, too, becomes a "new" species. Nonetheless, assume that seeds of an African tree, for example, were blown to St. Helena Island, where they were picked up and planted by Napoleon in 1817 or 1818. If and when they diverge to the species level are we to suppose that the African tree, which continues on virtually unchanged, is to be designated a new species also? At what point in time is this to be done? Some trees in China and the Appalachians are so similar after many millions of years of separation that they may still represent only subspecies.

Related species are kept from interbreeding by so-called (reproductive) isolating mechanisms. These are of 2 chief kinds: pre-zygotic (pre-mating) and post-zygotic (post-mating). Pre-zygotic barriers include vocalizations, odours (pheromones), 'courtship' displays (birds, fruit flies), and even patterns of light flashes (fireflies, Lampyridae). Such mechanisms seem insubstantial and indeed may begin as non-genetic variations, e.g. song dialects among birds. If isolation continues and is sufficient, they will acquire genetic bases; in the same period of time other distinctions will arise and, if secondary contact between 2 such groups occurs, may act as supplementary isolating mechanisms.

Post-zygotic isolating mechanisms run the gamut from complete sterility, through sterile hybrids (e.g. mules), to more or less fertile hybrids which, however, may possess subtle disadvantages in nature. In all such cases natural selection will tend to reduce costly mis-matings, which leave no long-term, viable offspring and which may even result in hardy 'mules' that compete with both parent species. An exceptional case is provided by certain flightless, very sedentary, Morabine grasshoppers in Australia, populations of which are prone to acquire chromosomal alterations. When such populations meet parapatrically, they interbreed freely; there has not been time for pre-mating barriers to evolve (White 1978, Key 1968). If 2 such subpopulations prove intersterile, speciation has occurred (called 'stasipatric' speciation); if some genetic interchange is possible, they are megasubspecies.

The opposite occurs more commonly. Isolated populations gradually acquire differences that will later serve as pre-zygotic isolating mechanisms (in voice, odour, behaviour, etc.) before genetic changes are sufficient to ensure sterility (post-zygotic separation). When such populations come into secondary contact, cross-breeding will be rare; but when it does occur, more or less fertile hybrids may result.

A few instances are known in which normally reproductively isolated taxa, though not intersterile, for example on isolated mountains or on islands, have produced hybrid swarms (Short 1969: 96–97). This suggests that the hybrids may be superior under the insular conditions, that pre-zygotic isolating mechanisms are incompletely developed (or break down), and that post-zygotic isolating mechanisms are lacking.

Two Mexican finches, *Pipilo erythrophthalmus* and *ocai*, interbreed in most areas where they meet, but are sympatric without interbreeding in one area (Sibley 1954, Sibley & Sibley 1969). In a few other cases supposed species (allospecies) are being hybridized out of existence: hybrids and one of the parental species apparently are being selected for at the expense of the second species, e.g. the new Zealand Black Stilt *Himantopus novaezealandiae*, is being displaced by the Common Stilt *H. himantopus leucocephalus* (Pierce 1984) and the Black-eared Miner *Manorina melanotis* by the Yellow-throated Miner *M. flavigula* in Australia (R. Schodde and L. L. Short *pers. obs.*). In both cases there has been extensive modification of the environment by humans. It can logically be argued that in such cases the taxa are megasubspecies and not allospecies, because otherwise the presence of effective isolating mechanisms should make massive hybridization impossible between species. Extinction by hybridization should not occur in allospecies; if extinction does occur after secondary contract, it is because one of the allospecies proves to be selectively superior to the other and replaces (total extinction) or displaces (partial extinction) it through competitive exclusion.

There may be rare exceptions, e.g. an allospecies restricted to an island subject to extensive human modification, followed by secondary entry by an allospecies, could result in hybridization and breakdown. It is even possible that a hybrid swarm could be the end product of the evolution of 2 allospecies if all populations of those allospecies became extinct other than the hybrid swarm itself. It is significant that polyploid species of plants, or more rarely parthenogenic species of animals (lizards), survive, when they do, in ecotypes which have been much disturbed (usually by man).

Competing Species Concepts. As noted, a continuing flurry of publications on the species question has promulgated several different species concepts or definitions (Andersson 1990). While our approach is practical rather than theoretical, the species is so central to taxonomy and classification that it is desirable to discuss briefly some of these proposals as they relate to our proposed terminology. Aside from other publications cited herein, one may *inter alia* mention important ones by Chandler & Gromko (1989), Coyne *et al.* (1988) and Häuser (1987).

(a) *Evolutionary species*. Simpson (1961: 153), primarily a palaeontologist, proposed the following definition: "An evolutionary species is a lineage (an ancestor-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." The word lineage implies an interbreeding population, viewed over time. Thus the definition again comes down to *genetically* isolated populations. Indeed, Simpson stated that in an earlier published version of this definition he had included the word "interbreeding" but dropped it to include clones and asexual "species" (but see below).

With the inclusion of the element of interbreeding, the evolutionary species definition becomes equivalent to the biological one. It does emphasize the temporal element: that species (and life) are a succession of individuals and populations. Indeed, only these 2 definitions are readily applicable to fossil as well as extant taxa. It further emphasizes that species have roles and tendencies, and as noted below that they have individual ecological niches. This need not be appended to the definition.

(b) *'Ecological' species concept*. Mayr (1982c: 273) and others (Hengeveld 1988) have added to the species definition that each species will have its own unique ecological niche. Simpson's "evolutionary" definition has ecological implications, while Van Valen (1976) also casts a species definition in ecological terms. Sympatric species, no matter how similar (sibling species) may be assumed to have ecological (niche) distinctions (Gause's principle). Yet there would seem to be no theoretical reason why allopatric species need differ ecologically. An insectivorous mole, *Talpa*, on one island and a marsupial mole, *Notoryctes*, on another, might in theory occupy identical ecological niches, yet they would be not merely different species but belong to separate sub-classes of Mammalia. No stipulation about ecology is needed in the species definition.

Somewhat similar is the occasional statement that speciation has not been "completed" until the 2 allied taxa have acquired overlapping (sympatric) ranges, which derives from the simple and pragmatically useful fact that sympatry provides the ultimate test for the efficacy of reproductive isolating mechanisms. If speciation is not complete when 2 allospecies happen to come into secondary contact, it may undergo refinement and reinforcement during parapatry and limited sympatry (e.g. the *Passerina* bunting case discussed below). Some parapatric species remain too similar ecologically to overlap; each of course is apt to be better adapted to a distinct microecotype within the main part of its range. In a few cases a new species may deviate so far ecologically from its immediate ancestors or nearest allies that overlap is out of the question, e.g. the first cetacean to become independent of land.

(c) *'Recognition' species concept*. Paterson (1985) concluded that the important element in species formation is not how individuals of a species avoid mating with those of other species but how they recognize individuals of their own. The former he calls the "isolation concept" and thinks it needs replacing. Others (e.g. Mayr 1986) regard these as 2 sides of the same coin: e.g. a male moth is attracted by pheromones emitted by females of his own species and ignores those of others. In plants and many lower animals recognition consists of reacting to another individual with the "right chemistry." "Recognition" may be by only one sex; male Pin-tailed Whydahs *Vidua macroura* and Straw-tailed Whydahs *V. fischeri* court any small brown bird that approaches, even unrelated serins *Serinus* spp.; further the 2 whydahs maintain interspecific territories, but their females only breed with the "correct" males (Short & Horne, *pers. obs.*). In sympatry, species are self-defining and thus are the only self-defining evolutionary unit. Taxonomists search for areas of sympatry between closely related taxa as the ultimate test of their status as species, allospecies or megasubspecies, and in order to gain insight into the nature of differences that obtain between related but allopatric taxa, the better to evaluate their status.

Isolating mechanisms vary, and under stress (lack of appropriate conspecifics, as in captivity), interbreeding often occurs between species never, or very rarely, known to hybridize in the wild. Also there are situations involving dynamic interactions of allospecies as they initially come into secondary contact, in which hybrids occur commonly at first, and then, as sympatry increases, hybridization ceases. An example is the movement of the Syrian Woodpecker *Picoides syriacus* into the central European range of its allospecies, the Great Spotted Woodpecker *Picoides major* (Bauer 1957). Such biological "mistakes" (due to lack of post-zygotic isolating mechanisms and breakdown of pre-zygotic isolating mechanisms), which may occur when the expanding species is rare and its potential conspecific mates are few, should not be interpreted to mean that the 2 taxa involved are conspecific. Sometimes, of course, a time span is required to be certain. In these cases strict application of Paterson's concept would mean that, when initially interbreeding, these taxa would be conspecific, but when hybridization ceased they would "become" species. Paterson's work will, however, bring more attention to the evolution of the crucial isolating stimuli involved in speciation. It should also prompt research on other forms of species recognition.

The species recognition associated with reproductive isolation of species is not unique to that facet of biology, nor is it always successful. African estrildine finches have characteristic, species-specific gape markings as nestlings, but nestlings of nest-parasitic widowbirds (*Vidua* spp.) mimic the gape markings of these estrildine nestlings, species for species, thus making it possible for the widowbirds to use the estrildines as foster parents for their own young (Payne 1982).

Interspecific territoriality is akin to recognizing other species as if they were conspecific and is thus a failure to show "species recognition", or rather is a broadening of the "recognition" to include other species. Many sophisticated adaptations have evolved for recognition of prey or host organisms (as by parasitic wasps, and nest-parasitic cuckoos), and of food plants by insect larvae and their adult forms, to give only a few examples. Within species there may be failure of "species recognition", as by birds of different local song dialects, that deter interbreeding of conspecific individuals of different demes (Payne 1986). Females of many species regularly reject as mates males in subadult plumage attempting to breed.

The biological species definition includes all aspects of the recognition of conspecific mates. It is thus inappropriate to designate the biological species concept as the "isolation" concept, either as a substitution for it or to compare it with the species recognition concept. For further discussion of Paterson's species recognition concept see Bock (1986: 41), Coyne *et al.* (1988), Häuser (1987), and Raubenheimer & Crowe (1987).

(d) *"Cohesion species concept"*. Templeton (1989: 12) wrote: "The cohesion concept species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms." He then tabulates these mechanisms. We need not reproduce his table, because the final product is close to our understanding of the species. All species have cohesion and Templeton rightly emphasizes this. To some extent it partakes of the "homeostasis" mentioned at various points by Mayr (1963). One may note that no species, if subdivided spatially, is so *cohesive* as to prevent differentiation and eventual formation of a new species. Asexual "species" on the other hand are too "cohesive"; adaptive change can take place only by the replacement of entire populations, one mutation at a time.

Templeton designated his cohesion species concept to accommodate both sexual and asexual populations. As discussed elsewhere, we do not consider this feasible.

(e) "Phylogenetic" species concept. This was introduced by Rosen (1973, 1979) and followed by others including Nelson & Platnick (1981) and Cracraft (1983). The phylogenetic species was recently defined by Cracraft (1989: 34–35) as "An irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent." McKitrick & Zink (1988) recommended the phylogenetic species to ornithologists but gave nary an example of how they would apply it to any species as presently understood.

All more or less isolated subpopulations of a species acquire genetic differences, whether adaptive or by genetic drift. Founder populations would immediately qualify as "phylogenetic species"; their gene pool will differ from the larger one from which it has been drawn. Indeed DNA "fingerprinting", from one point of view, has reduced effective population size to a single individual. When such populations interbreed with neighbouring populations, or are capable of doing so, are they species? If so, one could easily find subpopulations of *Homo sapiens* that still, despite all the mixing that has gone on, qualify as "phylogenetic" species. Morphs of a single population may differ more than will many such phylogenetic species. In the White-throated Sparrow *Zonotrichia albicollis* for example, 2 morphs differ in colour, in osteology, and chromosomally, as well as in habitat preferences and song frequency (Thorneycroft 1966, 1975). Yet they are only morphs; individuals of one morph prefer to mate with the other. Mayr (1963: 247) listed a number of genera, including the lowly *Asellus*, in which morphs differ in habitat preference (and doubtless in other ways as well).

Avise & Ball (1990) also emphasize that the number of subpopulations diagnosable by molecular biology or even phenotypically is enormous. Further, if analyzed by differing techniques or for varying goals, the boundaries of these subpopulations will often not coincide. The many well established breeds and varieties of domestic animals (dogs, pigeons, etc.) or cultivars and varieties of plants (roses, tomatoes, etc.) are phylogenetic "species". They are kept separate by the hand of man; their counterparts in nature by spatial isolation.

Presented with the males and females of a highly dimorphic species (e.g. the sapsucker *Sphyrapicus thyroideus*) in which the sexes are easily diagnosed phenotypically—by the sex chromosomes and presumably (if they could be demonstrated) by certain genes controlling the dimorphism—how would one determine that they belong to the same species? *Because they interbreed.* Much molecular biology is based upon tissues of a few individuals. How does one know that the other individuals assigned to a species based on such samples belong to it? Again, because they *interbreed*, or are assumed to do so because of the phenotypic uniformity bestowed by interbreeding. Thus, we are again back to the interbreeding test for the species.

J. Fitzpatrick, quoted by McKitrick & Zink, estimated that the Florida Scrub Jay *Aphelocoma c. coerulescens*, itself an outlier of a western species, might have to be divided into 2 or 3 hundred species. This may have been tongue in cheek but is hardly an exaggeration. This multiplication of species would conceal, not reveal relationships. For example, if the geographically variable Song Sparrow *Melospiza melodia* were split into 30 'species', the related, less variable, *bona fide* species, the Lincoln's

Sparrow *Melospiza lincolni*, and the Swamp Sparrow *M. georgiana*, would tend to be lost in the shuffle.

Many such species would be undiagnosable in traditional museum practice; all old specimens would have to be identified subjectively and assigned to their species on geographic bases. Some of these might represent "temporal" species, because of biochemical evolution in the past 50 to 150 years after the type series and other museum material was collected. Fossil material would have to be ignored, or included subjectively.

We thus conclude that the proposal to call every diagnosable population a *species* is wrong in both fact and theory and would lead to chaos in application. That we are not overstating this point will be appreciated by those concerned with conservation decisions of governmental agencies, and the economics of conservation to the lay public, if they had to defend the preservation of every phylogenetic "species".

None of the above is meant to impugn the value of genetic and biochemical research in casting light on fundamental problems. If such research reveals an out-and-out error, as Zink (1988) has done in the *Pipilo crissalis*/*P. fuscus* group of finches, and this is supported by other data, by all means alter the classification to correspond with the newly discovered facts.

Practical considerations. How can a species be defined in terms of breeding behaviour when for all fossil species and many living ones, e.g. deep-sea fishes, we know nothing of breeding behaviour? The short answer is that biology is the science of life; species are populations of living organisms and there is no escape from this dilemma. Fortunately interbreeding and heredity do impart a certain uniformity to species. With most groups, given a mixed bag of specimens, one can sort them out into species with few errors. One may, to be sure, be misled by differences due to sex, age, castes, morphs or life stages, but this would be true whatever species concept was used. Once such problems have been surmounted, the identification of sympatric species usually offers no special problems. Some sibling species, especially among invertebrates, may, to be sure, remain unmasked until studied in the field or found in the laboratory to be inter-sterile.

Sympatric populations that do not interbreed, or not to an extent that undermines their genetic integrity, are perforce species. Closely allied species which have only recently or partially achieved sympatry may interact in various ways (limited hybridization, interspecific territoriality, or displacement of one by the other in some areas and not in others).

Parapatric populations present greater difficulties, but if they don't interbreed they are species, usually allospecies; if they do, they are subspecies. When limited or sporadic interbreeding occurs, the analysis must be more in depth; Short (1969, 1972) has presented procedures and guidelines for analyzing such cases. In general, if selection is reducing hybridization parapatrics are species, but not so if the reverse occurs. Often a long-term study is needed to find out, especially where parapatry is very limited. Most such instances are of secondary contact after evolution in isolation; it is doubtful whether primarily parapatric subspecies can advance to species status, except perhaps where there is an increasingly sharp break in their ecotypes. Many parapatric species meet along ecological gradients, but even if the change is very gradual, the 2 may abut sharply (e.g. see Short 1971 for 2 woodpeckers, *Picoides nuttallii* and *P. scalaris*, in the American Southwest). Rarely, as in the crows *Corvus corone* and '*C. cornix*' of Europe (Kryukov & Blinov 1989), a narrow but spatially shifting hybrid zone persists; this should not be taken to infer that they are allospecies. In this case the narrowness of the zone and its shifts reflect forces of selection and environmental gradients that are commonly found intraspecifically, and usually are inconspicuous, but in this example are conspicuous (the 2 crows are all-black vs black and grey). For example, there is a marked shift in tail-spotting of eastern and western populations of the American Robin *Turdus migratorius* over a few-score kilometers in the Great Plains, whereas the crows are megasubspecies, freely interbreeding throughout and are thus separated and yet connected by the hybrid zone. In an altitudinal transect in New Guinea, Diamond (1972: 27) found several pairs of species replacing each other abruptly, not always at the same altitudes; nor are all such pairs allospecies, though usually congeneric. The barbets *Pogoniulus pusillus* and *P. bilineatus*, not each other's nearest relative, occur sympatrically in some African habitats; in others there is an altitudinal replacement, and still elsewhere the bird of lower elevation extends to higher elevations in the absence of the second species (Short & Horne 1988). Sometimes an area is found between interbreeding allospecies where neither of them breeds, as in the titmice *Parus atricapillus* and *P. carolinensis* in some parts of their ranges (Brewer 1963).

When taxa doubtful as to subspecies or species are spatially disjunct the problem is more difficult. Vast numbers of populations are isolated in this way, on islands, in lakes, and on mountain tops. To each such case the taxonomist must bring all available data from study of congeneric or allied species and subspecies and the gaps between them; differences have to be sought in such possible isolating mechanisms as voice, behaviour, vagility, and others. Sometimes field or laboratory experiments are possible. Mayr (1969) provided a methodology for the evaluation of such taxa. Following analysis of information from all available sources, the taxonomist reaches a verdict as to the status of the disjunct populations. The verdict, to be sure, may be somewhat subjective or tentative, but an equally important result of the process is the enhancement of knowledge gained about the characteristics and biology of the organisms.

In summary, the taxonomist working with a relatively localized fauna or flora will usually encounter rather few problems as to species discrimination. When working with widespread groups, especially those with disjunct populations in varied habitats, it is the often the rule rather than the exception to encounter populations near the megasubspecies-allospecies boundary which require a judgmental verdict.

9, 10—MONOTYPIC SPECIES; POLYTYPIC SPECIES

These are are well known terms for designating species lacking recognized subspecies (monotypic) and species having recognized subspecies (polytypic).

11—MESOSPECIES*

This term is here proposed for polytypic species none of whose subspecies are deemed to be approaching species status. That is, it includes all those polytypic species, usually a large majority in any group of organisms, that are not megaspecies. Mesospecies, like megaspecies and superspecies, must be evaluated at one point in time, almost always the present.

12—MEGASPECIES

Crawford-Cabral (1986) proposed this term for species composed of megasubspecies. He employed the megaspecies in analyzing the evolution and zoogeography of a group of Rodentia as represented in the fauna of Angola, Africa.

Are all species that contain one megasubspecies comprised entirely of megaspecies? In a species such as the Northern Harrier *Circus cyaneus*, in which one megasubspecies occupies Eurasia and the other North America, that is obviously the case. But what of a species such as the Savannah Sparrow *Passerculus sandwichensis*, in which there is a megasubspecies *Passerculus* (*sandwichensis*) *princeps* on tiny Sable Island, off the coast of Nova Scotia, while elsewhere the species occupies most of North America, where it is separated into several lesser subspecies of the rank here named mesosubspecies? Almost surely, *princeps*, long regarded as a full species, is a recent post-glacial offshoot of the mainland population. Nevertheless, we conclude that the mainland population ranging from Alaska and Labrador to California should be called a megasubspecies, *P.* (*sandwichensis*) *sandwichensis*. If it and *princeps* were to attain species status, the step over the species threshold would probably not occur as a result of genetic changes in the mainland population, but rather in the small, isolated population of *princeps* itself, but this is not certain. For our purposes, this situation has been presented in oversimplified form, for there actually are 3 subspecies of *P. sandwichensis* along the coast of southern California and adjacent Mexico which, while not as strongly differentiated as *princeps*, nevertheless were at one time considered to be one or even 2 additional species. These 3 subspecies comprise a third megasubspecies, *P.* (*sandwichensis*) *rostratus*. Thus, the picture becomes more balanced, with a megasubspecies on or near each coast and the third occupying the intervening continent (Zink *et al.* 1991).

In our 1976 paper introducing the megasubspecies we did in fact conclude that conferring that status on one unit of a species automatically confers that status on the other population(s). Thus we wrote (1976: 163): "Although the term megasubspecies would often refer to a population occupying a small range, as on an island, this status confers like status on the remaining group or groups . . . of populations."

We have minimized our use of the term "sister" taxa, because it is a cladistic term that most cladists restrict to *only* 2 taxa. Yet we know that there frequently are more than 2 megasubspecies in a megaspecies, or allospecies in a superspecies. To be sure, it cannot be demonstrated that the allospecies in a superspecies, when more than 2, split simultaneously. For all practical purposes, however, one may assume that they did; such assumptions are as nothing compared with those often made when fossil taxa that diverged aeons ago are considered as sister groups. In any case the exact points of bifurcation are apt to be so close in time as to be essentially simultaneous.

A major fault of the cladistic approach, in our view, stems from the very fact that taxonomic status is determined strictly by the branching (furcation) points, and differentiation is ignored or discounted. Yet there are many cases (e.g. Haffer 1974 pointed out a number of them) in which 3, 4 or even 5 forms evolved from a common ancestor, with their evolutionary history predicated (in this case) upon vicariant separation, such as a developing system of rivers about the Amazon, or fragmentation of forest by drought. If the result is 5 approximately equally divergent entities, we would consider all 5 as coequal mesosubspecies, megasubspecies or allospecies depending upon their degree of differentiation and our judgment concerning their reproductive isolation. Were all 5 to have originated exactly simultaneously, their divergence from that point would make it extremely unlikely that their simultaneous origin could ever be deduced from their morphology. Even if geological data allowed one to construct a 'true' cladogram, this would not necessarily be useful (differences in time between branchings may only be several hundreds of years); indeed, the last 2 populations to branch, by chance alone, might now be more divergent than are the others that separated somewhat earlier. Hence cladistic analyses are liable to indicate incorrectly the bifurcation of the taxa. Thus it seems appropriate to treat the 5 as coequal taxa.

Short *et al.* (1983) described such a case among 5 megasubspecies of Australian sitellas (*Daphoenositta chrysoptera*), all of which come together and interbreed, forming a 5-way hybrid zone in central Queensland. The determination of time factors in this divergence, as in many cases, is very difficult; and the analysis of their divergence through study of morphology is complicated by the evolution of 'white-headedness' in the megasubspecies *leucocephala*, which has obliterated various features of colour pattern useful in the other 4. The 5 taxa appear behaviourally alike and they are vocally not distinguishable (Short & Horne, *pers. obs.*). Since all 5 hybridize *inter se* to the same extent, there appear to be no incipient isolating mechanisms in any one of them. Cracraft (1989) treats these sittellas very differently, using the phylogenetic species concept. He disregards the fact that the 5 are vocally similar if not identical, and the mesosubspecies that are also found among some of the 5 megasubspecies. Using primitive-derived character states that apparently are put forward *ad hoc* (some of his characters are affected, for example, by albinism in *leucocephala*, and for others there is simply no indication of which condition is 'derived'), he treats all 5 as 'species' and presents a cladogram of supposed relationships among the 5 for which we see no historical or morphological bases. In addition he ignores the extensive hybridization among the 5 diverse 'species'. The resulting products of interbreeding perforce become 'interspecific' hybrids. These occupy large areas and number tens if not hundreds of thousands of individuals. It is misleading to consider the 5 taxa as anything but coequal megasubspecies. Since the geological data often are unavailable or controversial in such cases, cladists may proceed by subjectively designating branching points based upon morphology and degree of divergence, thus producing a branching hierarchy (cladogram) which may be completely in error. As noted, the same considerations apply to allospecies.

13—ISOSPECIES*

We introduce this new term to designate a species that is not a member (allospecies) of an existing superspecies, that is, has no contemporary sister species. To be sure, many such species evolved as allospecies of a superspecies whose other members have become extinct, or, in some instances, may have evolved into new superspecies with their own contained allospecies. Chance events such as presence or absence of barriers, or differing rates of evolution, could bring about such a result. In other instances an isospecies may arise as a result of phyletic evolution.

14—ALLOSPECIES

Since an allospecies is one component of a superspecies, see also the discussion of that unit. Having concluded that both disjunct and parapatric taxa should be subsumed under allopatry, we disagree with Prigogine (1984, 1985), who limited the term allospecies to disjunct taxa and call those whose ranges are in contact 'paraspecies'.

Priogogine's 'paraspecies' is just one of many descriptive and potentially confusing labels that could be applied with reference only to the presence and amount of contact which obtains between allospecies. One could, for example, give 'allospecies' different names depending upon how far apart they are geographically, or 'paraspecies' likewise based on the extent of their contact, or differentiate between 'partly sympatric allospecies' as to the extent of their sympatry (small, moderate). Any or all of such distinctions would result in confusion. It matters greatly in analysis whether parapatric contact occurs along an interface 100 m, 100 km or 1000 km long, but such information should not be brought into definitions of taxa. Indeed the extent of parapatry and whether or not some sympatry occurs throughout a long, more or less abutting area of contact usually is incompletely known, and often is inferred from very few sites. Determination of parapatry requires one to verify that individuals of 2 allopatric populations can make contact in the breeding season. This requires that the observer is at the right place at the right time, particularly in cases of altitudinal parapatry, as non-breeders may wander out of the breeding range. We prefer to use 'allospecies' as above, whether the allospecies are disjunct, parapatric or (usually marginally) sympatric. Except that subspecies cannot be sympatric, we note that the same confusing terminology could be used for them—for example, various terms could be applied, such as 'parasubspecies' and 'allosubspecies'; such terms we think would be ill-advised. It seems better to restrict the number of terms and to have them refer to important levels of speciation intrinsic to the taxa, and thus not based upon chance extrinsic factors; then they will be of broader utility.

In parapatric allospecies, sporadic, marginal, or temporary overlap is probably the rule rather than the exception. Also, allospecies may be broadly sympatric in the off-season. Sometimes, as noted above, there may be a narrow zone between two allospecies in which neither occurs. More commonly, small, transient colonies of one or the other of a pair of allospecies exist within the boundaries of the other. In such situations, often in conjunction with a patchy environment, 2 allospecies (some would say former allospecies) are now sympatric over considerable areas, although the actual contacts, because of environmental preferences, may be hardly greater than in more conventionally parapatric species. The Eastern (*Sturnella magna*) and Western (*S. neglecta*) Meadowlarks studied by Lanyon (1957, 1962, 1966) are sibling species, have no close relatives, differ greatly in song and alarm notes, and overlap over a wide zone in central North America. There is occasional ineffective hybridization. The Indigo (*Passerina cyanea*) and Lazuli (*P. amoena*) Buntings provide a similar example (Sibley & Short 1959), with more hybridization and expanding overlap; eastern *cyanea* now appears in pockets far into the western North American range of *amoena*. Clearly these are or were allospecies, and their interactions and those of similar pairs provide excellent object-lessons for analyzing various aspects of speciation. Such forms, still able to interbreed and interacting ecologically with increased sympatry (ecological separation, interspecific territoriality) might be designated 'emergent allospecies'. This could be applied as well to cases of expansion of one allospecies into the range of another, with hybridization restricted to the advancing forward line of the invading allospecies, after which interbreeding is much reduced or ceases, the forms being in partial sympatry (e.g. the woodpeckers *Picoides syriacus/major* mentioned above and the titmice *Parus cyaneus/caeruleus* in Europe, discussed by Short 1969: 90–91; see Hewitt 1989).

Another remarkably complex case is afforded by 2 wood-warblers, *Vermivora pinus* and *V. chrysoptera*, which occur in patchy habitat over much of eastern North America (Gill 1987). They are sympatric in some areas and allopatric in others. Though the species' identities are not undermined, the 2 hybridize fairly freely, producing an array of hybrid phenotypes, 2 of which are so frequent and so distinct that they were described as species. *Vermivora pinus* is moving northwards, usually replacing *chrysoptera*, but with at least one pocket of the latter "left behind" in somewhat atypical habitat (Frech & Confer 1987). As a further complication occasional individuals learn the song of the 'wrong' species.

The behavioural interactions, general similarity, and occasional hybridization in such pairs demonstrate that they are allospecies. Careful analysis and weighing of evidence is necessary in determining their status and what they reveal about the dynamics of speciation and allied processes. Expanding allospecies with overlap but still some hybridization may be approaching the limit of allospecies, but with 'backward' shifts still possible, perhaps due to man's persistent modification of the environment.

The attention given to such taxa reflects their importance. One difficulty in considering partly sympatric pairs to be (still) allospecies is that in sympatry they may be mixed, and possibly confused with, species that are still interacting 'sexually' and ecologically in one way or another, but which are beyond the point where they can be properly called allospecies. Broadly overlapping congeneric species, perhaps formerly allospecies, may interact to some degree, and even species representing different genera can interact strongly, appearing like emergent (congeneric) allospecies. For example 2 wrens, *Thryomanes bewickii* and *Troglodytes* *aedon*, still hold interspecific territories, even though they are usually placed in different genera (Root 1969). Some might prefer to use Ripley's (1945: 338) term "interspecies" pair or group in such cases until their interactions have been well-studied and their relationships are clarified.

As noted earlier, the analysis of disjunct, closely allied taxa is difficult and sometimes subjective. Still, the gamut of possible shades of relationships is the same for disjunct, parapatric and partly sympatric sister taxa; what differs critically among them are the possibilities for interactions, and these determine the amounts and kinds of data they can provide, and the techniques that are available for studying them.

15—SIBLING SPECIES

Sibling species are ones that are difficult to distinguish phenotypically, such as the Eastern and Western Meadowlarks mentioned above. They will almost certainly belong to the same genus, but may not necessarily be the most closely related species within the genus, though that will often be the case. The classic example is of the fruit flies *Drosophila pseudoobscura* and *D. persimilis*, which can be separated phenotypically only by refined statistical analysis of measurements from large samples. Yet these 2 are completely cross-sterile and hence *ipso facto* species. Such sibling species are being unmasked commonly among insects; they exist but in far smaller numbers in vertebrates. The term is subjective and largely one of convenience and there is no 'test' or absolute criterion for sibling species. They may be either sympatric or allopatric, but the sympatric ones receive the most attention because they immediately pose problems as to how such at least superficially similar species can coexist. Allopatric sibling species are less apt to be detected unless it is found by chance that they are intersterile. In a few cases among birds, for example the many all-black crows and ravens of the widespread genus *Corvus*, there are numbers of both allopatric and sympatric sibling species.

Many sibling species evolve as an end result of divergence in isolation, and only later (sometimes) become sympatric; their antecedents, ranging from demes to megasubspecies, must be even more difficult to detect. The antecedent populations would not fulfill the requirement for formal subspecies since they would probably not be 'visibly different'. As a practical matter, it seems unwise to name such 'proto-sibling species' when they are suspected. There is a special challenge to the taxonomist to evaluate allopatric populations very carefully in groups well known to have sibling species, for example, among birds: *Corvus*; larks, Alaudidae; tyrant-flycatchers, Tyrannidae; and bulbuls, Pycnonotidae.

The 8 terms here advocated for various species-level taxa are not all mutually exclusive. A species may be monotypic or polytypic (but not both). A polytypic species may be either an isospecies or a mesospecies or a megaspecies. An isospecies cannot also be an allospecies, but an isospecies or an allospecies can also be a monotypic species, or a mesospecies, or a megaspecies. In theory, any of the others could be a sibling species.

16—GENUS

Higher classification is based upon the grouping of species in clusters of varying degrees of relationship, and is thus a scheme of hierarchies in the

Linnaean system of classification (genus, tribe, subfamily, etc.). These hierarchies are a result of evolution, with its speciation, adaptive radiations and extinctions. Thus higher classification is based on reality; but it also has a subjective element in that each cluster of species is, to a degree, unique. It is a matter of opinion as to how closely related a group of species must be to constitute a genus or a group of genera to constitute a family. Some species are so distantly related to any contemporary ones that they are best left in monotypic genera. For 'splitters' (taxonomists using many small genera) or 'lumpers' (those employing very broad genera) one can only counsel moderation. The genus has as its only function (aside from reducing the number of species names required), that of indicating groups of related species, but it must not be so inclusive as to impinge on the next higher category (tribe, subfamily, family). Nor can the number of categories be arbitrarily established; above we mentioned one, the tribe, not used by Linnaeus. The genus and subgenus, however, are 'official' categories, with established rules for their nomenclature.

The binomial system does have one serious flaw: changes in the genus' name affect both biologists and the general public. Yet new information as to a species' relationships may make nomenclatural changes mandatory; honest differences of opinion may do the same, e.g. one taxonomist being more impressed by certain morphological, behavioural or other peculiarities of a species, perhaps considering it as a monotypic genus, than is another who allows for more differences among congeneric species). Again, one can only recommend holding changes to a minimum; official check-lists, revised occasionally, help. More drastic solutions, such as using very broad genera and conducting the finer details at the subgenus level (Amadon 1966a) or using a mononomial system (Michener 1964) have met with little interest. Numerical systems may, to be sure, be used with computers (Little 1964), but names are needed also: it is easier to remember a hundred names, even Latin ones, than 4 or 5 numbers replacing a name.

One should attempt to keep the criteria for genera and other higher categories consistent across groups and time. This has heuristic value in that, e.g., a list of the species in an ecotype will contain genera that are roughly equivalent for plants and animals. Likewise fossil biotas, which often consist of a mixture of extinct and living species, can be meaningfully compared as a unit or with other biotas, and included with them in classifications.

Perhaps it is worth stressing the obligation of the systematist to place his studies in perspective by considering the next higher and next lower category to that with which he is dealing. That is, species of a genus ought not to be studied or revised without considering the taxonomy of related genera, and the final results ought to take them into account. A genus (or species, or family) should not be studied, as it were, in a vacuum. Likewise, although political or economic factors sometimes force a narrow focus upon a taxonomic investigation, studies that are geographically restricted (to a state, country or region), although the taxa involved are widespread outside that restricted area, should sometimes be postponed. Caution is especially advised when working with a taxon at the fringe of its range, or taxa which are at the periphery of the range of the group to which they belong. If avoidable, a speciose tropical genus should not be revised if one can study in detail only a handful of its species which marginally penetrate an adjacent temperate region.

17—SUBGENUS

The subgenus is a formal category and if one recognizes subgenera in a genus then all of its species should be assigned to one subgenus or another, according to their affinities. A systematist revising a genus containing some little known or problematic species may prefer to avoid this formal category and use the informal species group; then species presenting such problems may, so to speak, be left 'dangling' without the necessity of assigning them formally. It is better to employ subgenera than to oversplit genera. In groups in which many genera were named that now seem superfluous, such names are often available for subgenera. It is unwise to use subgenera in some genera of a family but not in other equally diverse ones, though if some are much better known than others this may ensue. A few taxonomists go to the extreme of decrying generic 'splitting', meanwhile flooding the literature with subgenera.

18—POLYTYPIC GENUS

As defined—a genus containing more than one species.

19—MONOTYPIC GENUS

The genus is defined as a group of species; hence a genus with but one species seems like a contradiction in terms. Nonetheless, some species, indeed considerable numbers in certain groups, are so distinct and lacking in close relatives that they must be admitted as monotypic genera. If we had a complete fossil record some of them would be found to have contained other species now extinct. Indeed many monotypic genera are relicts, but some of them may have contained but one species for a very long time, e.g. *Gingko, Latimeria* and *Sphenodon*. Still others are probably the end products of phyletic evolution and never contained other species. Among birds, *Balaeniceps* or *Rhynochetos* might be candidates. Finally, during adaptive radiations, species may evolve with relative rapidity, thereby producing monotypic genera that may or may not later bud off additional species. Thus, at any point in time some species have very close relatives, others only very remote ones, while the majority fall between.

20—QUASI-MONOTYPIC GENUS

This term was coined by Amadon (1968) but the concept has been employed by others (e.g. Diamond 1972: 305). Many genera consist of a single superspecies and are, for some biogeographical purposes, equivalent to a single species. Thus the skimmers, *Rynchops*, a superspecies with 3 species, 1 in Africa, 1 in India, and 1 in the Americas, are so similar and specialized that it is unlikely that sympatry will ever ensue; this genus is quasi-monotypic.

21—SPECIES GROUP

The species group might be regarded as an informal, un-named subgenus. Because it is informal, not all the species in a genus have to be assigned to a species group and indeed the information is often lacking to do so. With further data, species groups in a genus may be replaced by formal subgenera, or this may be deemed unnecessary. Obviously, use of the species group does not burden the memory with more names (usually a species group is referred to by the specific name of one of its best known or widespread species). The purpose of both categories, of course, is to aid in understanding relationships and lines of evolution, especially in species-rich genera (see Mayr & Short 1970: 102–103).

Paramount is the point that the species in a group are more closely related, often considerably more closely related, to one another than is any of them to any other species in the genus outside the group. It is implicit that there are gaps between species groups. In very large genera, it sometimes may be desirable to set up species groups within subgenera.

Haffer (1986a) has more rigorously, and we feel unnecessarily, redefined species groups to equate them with putative former superspecies whose component species are actually or potentially sympatric. This would severely limit the use of species groups because allopatric species (that were formerly all allospecies of a superspecies) can evolve further in isolation to the point at which their relationships are those of a species group (or, with one or more other sympatric or allopatric species, they may form a species group). Also a superspecies, or several superspecies, may form a species group together, or along with, one or more isospecies. Extinctions of species or allospecies may leave isospecies that are taxonomically somewhat isolated in their genus, though their relationships with other isospecies and superspecies may be sufficiently close to include them in a species group.

The barbet genus *Trachyphonus* contains 5 species interrelated as follows: (a) a species group *erythrocephalus-margaritatus-darnaudii*, of which the first 2 make a superspecies, while *darnaudii* is a megaspecies; (b) another megaspecies *purpuratus*; and finally (c) a mesospecies, *vaillantii* (Short & Horne 1985a,b, 1988). This illustrates the use of a species group in a way that would not be possible under Haffer's (1986a,b) proposal, by which we feel much is lost in encumbering and narrowing the use of 'species group'.

22—SUPERSPECIES (see also discussion of allospecies)

The allospecies of a superspecies are more closely allied to one another than to any other species. Some genera, subgenera or species groups consist of a single superspecies, but many contain species not so intimately related. Allospecies are often the equivalent of the cladist's 'sister species' (or for some, e.g. Cracraft 1989, 'sister megasubspecies').

In formal taxonomic treatments the use of brackets to indicate superspecies is recommended (Amadon 1966b). In other contexts this may be accomplished by using footnotes (A.O.U. 1983), by the use of braces (Short 1982), by connecting allospecies with hyphens (Diamond 1972: 321), or by the use of superscripts (Amadon & Bull 1988).

In listing allospecies of a superspecies, the first named allospecies does not always appear first, because of relationships, primitive-derived sequences, or geographical conventions. In some local or regional publications, not all of the allospecies in a superspecies may be listed. Still, it is often useful to know that a species has allospecies elsewhere. For example in a list of the bird species of Africa *Haliaeetus* [*vocifer*] indicates that *vocifer* has one or more closely related species (allospecies) elsewhere (in this case a species in Madagascar).

The designation of superspecies is often tentative. The Indian and African elephants do not form a superspecies, but without a fossil record that might not be so obvious. Question marks may be used to indicate doubt, or one may say "species 'X' and species 'Y' *may* constitute a superspecies". Such qualifications do not detract from the utility of the concept (Amadon 1966b, Mayr & Short 1970).

Haffer (1986b) has rigorously subdivided superspecies into 'First Order' superspecies (those we have discussed above); and 'Second Order' superspecies (or 'megasuperspecies'). The second order superspecies contain either 2 (or presumably more) of his first order superspecies, or a mixture of one (or more) first order superspecies with one (or more) species not part of a first order superspecies, i.e. with what we term isospecies. While every attempt to clarify and denote relationships is to be applauded, there is greater subjectivity in Haffer's approach; for example, one must guess about extinctions of former allospecies. We suppose one could go further, to 'Third Order' superspecies, and so on, but this would seem to compound the subjectivity at several levels, perhaps exponentially, with greater difficulty in distinguishing second order and third order superspecies, and even more potential for errors. We realize that many isospecies evolved as allospecies of superspecies whose sister allospecies became extinct. Proving this would indeed be difficult, as in the case of Haffer's (1986b, Fig. 1c) example of a second order superspecies formed from 2 first order superspecies, each of which apparently had suffered the extinction of one allospecies. By overly striving to be precise, Haffer has unduly restricted a more broadly useful terminology, coupled with the addition of greater subjectivity, and we think his categorizing of superspecies is not practical for general use. To be sure, specialists intensively studying a limited cluster of taxa may find it worthwhile to group them in various ways.

There has been an unfortunate tendency, evident, e.g. in Hall & Moreau (1970) and Snow (1978) to place all well-marked, congeneric, allopatric taxa into superspecies. This 'overinflation' of the superspecies, effectively to the level of the species group, has been criticized by Vande weghe (1988: 2550), indicating the crucial need to use all available information in making taxonomic decisions involving allopatric taxa. It is the task of the taxonomist to evaluate carefully all related allopatric taxa to determine whether they are monophyletic, and whether relationships are at the level of megasubspecies, superspecies, or species group. Faulty assignment of level (equivalent to 'upgrading' or 'downgrading') is wrong, no matter what the level, whether done intentionally (persons concerned about the conservation status of taxa may do this), or unintentionally (through failure to analyse appropriately the available data). Allopatry alone does not place a taxon in any one of these categories.

23—BIOGEOGRAPHICAL UNIT (or SPECIES)

This is the concept that is usually called a 'zoogeographical species'—one in which isospecies and superspecies are equated as biogeographic entities. That is, individual allospecies are not tallied separately. Since the concept applies equally well to plants, in which they would be called 'phytogeographic units', we suggest that biogeographic be used to cover both. Further, 'species' is somewhat misleading in this context, because superspecies, of course, are groups of species, not single species. We therefore believe the word 'unit' to be preferable.

As an example, assume that a chain of islands was colonized by 2 species of a family, the 2 not closely related (i.e. they represent different genera). Assume further that one of them is now a superspecies with 5 allospecies, each on its own island, while the second is still monotypic. If all the allospecies are tallied, it conceals the important fact that the family in question has colonized these islands only twice. Biogeographic units thus are useful in comparative studies of the diversity of different regions, and continents, as well as diversity of different groups within and between regions (see Mayr & Short 1970: 5).

In his check-list of the Pipridae and of the Cotingidae and elsewhere Snow (1979, see footnotes) equated 'zoogeographical species' with 'superspecies', citing Mayr & Short (1970). The latter, however, as we do here, treated zoogeographical species (or 'units') as including not only superspecies, but also non-allospecific species (isospecies). We feel that our usage and the distinction between zoogeographical units and superspecies have considerable heuristic value.

24—ASEXUAL POPULATIONS

The interchange of genes (e.g. 'conjugation' in *Paramecium*) apparently arose fairly early in the history of life and in higher organisms became sexual reproduction. The latter conferred such immense advantages by increasing heritable variability and hence adaptability that it has been dominant ever since (Vrijenhoek 1990). Nevertheless, some monocellular organisms (some bacteria) and a few advanced forms of life reproduce exclusively by asexual means. Most of them are plants and result from polyploidy; vegetative reproduction is much easier in plants and permits such sterile individuals to survive. Parthenogenic populations among animals are rarer, except for 'castes' in some social insects, but these are irrelevant here. Polyploids or sterile hybrids between species of animals have little chance of survival, but a few parthenogenic populations of lizards and other groups have managed to do so. Such instantaneously produced species, whether plant or animal, usually survive, when they do so, in raw, disturbed habitats (whether naturally so, or by humans), where competition is less.

Many species of plants, known by chromosome counts to have arisen by polyploidy, later again reproduce sexually. Occasionally fertile individuals do occur, and so great is the premium on genetic exchange that gametic reproduction has become re-established.

Are asexually reproducing populations or clones to be called species? Our preference would be to use some such term as 'pseudo-species' or 'quasi-species'. Nevertheless, so much literature, especially botanical, uses 'polyploid species' that we see little hope of a change. Hence one accepts a second major category of species to be called 'Asexual' or perhaps better 'Agametic' species. Other species are then Sexual or Gametic Species. The latter are so much more important and successful (except perhaps in some bacteria, viruses and the like) that the term species, without qualification, may be taken to refer to those in which an exchange of gametes occurs. If confusion arises, a simple alternative would be to agree that 'species' in quotation marks always refers to asexual populations.

Acknowledgements

The following have read one or another draft of this paper, with varying degrees of approval or disapproval, and made suggestions benefitting it: George Barrowclough, Walter J. Bock, John Bull, Niles Eldredge, Ned Johnson, Ernst Mayr, Guy Musser, François Vuilleumier.

References:

Amadon, D. 1966a. Another suggestion for stabilizing nomenclature. *Syst. Zool.* 15: 54–58.
— 1966b. The superspecies concept. *Syst. Zool.* 15: 245–249.
— 1968. Further remarks on the superspecies concept. *Syst. Zool.* 17: 345–346.
Amadon, D. & Bull, J. 1988. Hawks and owls of the world: a distributional and taxonomic list. *Proc. Western Found. Vertebrate Zool.* 3: 294–357.
Amadon, D. & Short, L. L. 1976. Treatment of subspecies approaching species status. *Syst. Zool.* 25: 161–167.
American Ornithologist's Union. 1983. *Check-list of North American Birds*, 6th ed. American Ornithologists' Union, Washington.
Andersson, L. 1990. The driving force: species concepts and ecology. *Taxon* 39: 375–382.
Avise, J. C. & Ball, R. M., Jr. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. Pp. 45–67 *in* D. Futuyma & J. Antonovic (eds.), *Oxford Survey Evol. Biol.* Vol. 7. Oxford University Press.
Barton, N. H. 1989. Founder effect speciation. Pp. 229–256 *In:* D. Otte & J. A. Endler (eds.), *Speciation and Its Consequences*. Sinauer Associates, Sunderland, Massachusetts.
Bauer, K. 1957. Zur systematischen Stellung des Blutspechten. Pp. 22–25 *in Deutschen Kulturbund*. Johann Friedrich Naumann-Ehrung, Leipzig.
Bock, W. J. 1986. Species concepts, speciation, and macroevolution. Pp. 31–57 *in* K. Watsuki, P. H. Raven & W. J. Bock (eds.), *Modern Aspects of Species*. University of Tokyo Press, Tokyo.
Brewer, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina chickadees. *Auk* 80: 9–47.
Bullough, W. S. 1942. The reproductive cycles of the British and continental races of the Starling. *Phil. Trans. Roy. Soc. London, Ser. B.* 231:165–246.
Carson, H. L. 1971. Speciation and the founder principle. *Stadtler Genetic Symp.* 3: 51–70.
— 1989. Genetic imbalance, realigned selection, and the origin of species. Pp. 345–362 *in* L. V. Giddings, K. Y. Kaneshiro & W. W. Anderson (eds.), *Genetics, Speciation and the Founder Principle*. Oxford Univ. Press, Oxford, U.K.
Chandler, C. R. & Gromko, M. H. 1989. On the relationship between species concepts and speciation processes. *Syst. Zool.* 38: 116–125.
Coyne, J. A., Orr, H. A. & Futuyma, D. 1988. Do we need a new species concept? *Syst. Zool.* 37: 190–200.
Cracraft, J. 1983. Species concepts and speciation analysis. Pp. 159–187 *in* R. F. Johnson (ed.), *Current Ornithology*, vol. 1. Plenum, New York.
— 1984. The terminology of allopatric speciation. *Syst. Zool.* 33: 115–116.
— 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of speciation. Pp. 28–59 *in* D. Otte & J. A. Endler (eds.), *Speciation and Its Consequences*. Sinauer Associates, Sunderland, Massachusetts.
Crawford-Cabral, J. 1986. A discussion of the taxa to be used in a zoogeographical analysis as illustrated in Angolan Muroidea. *Cimbebasia Ser. A.* 8: 161–166.
Diamond, J. M. 1972. Avifauna of the highlands of eastern New Guinea. *Publ. Nuttall. Orn. Cl.* 12.
Dobzhansky, T. 1950. Mendelian populations and their evolution. *Amer. Nat.* 84: 401–418.
Ereshefsky, M. 1989. Where is the species? Comments on the phylogenetic species concept. *Biol Philos.* 4: 89–96.
Frech, M. H. & Confer, J. L. 1987. The Golden-winged Warbler: competition with the Blue-winged Warbler and habitat selection in portions of southern, central and northern New York. *Kingbird* 37: 65–71.

Gill, F. B. 1987. Allozymes and genetic similarity of Blue-winged and Golden-winged warblers. *Auk* 104: 444–449.

Gould, S. J. & Eldredge, N. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiol.* 3: 115–151.

Haffer, J. 1974. Avian speciation in tropical South America. *Publ. Nuttall. Orn. Cl.* 14.

— 1986a. Über Superspezies bei Vögeln. *Ann. Naturhistor. Mus. Wien.* 88/89, B: 147–166.

— 1986b. Superspecies and species limits in vertebrates. *Z. Zool. System. u. Evolutionsforschung* 24: 169–190.

— 1987. Biogeography of neotropical birds. Pp. 105–150 *in* T. C. Whitmore & G. T. Prance (eds.), *Biogeography and Quaternary History in Tropical America.* Clarendon Press, Oxford.

Hall, B. P. & Moreau, R. E. 1970. *An Atlas of Speciation in African Passerine Birds.* British Museum (Nat. Hist.), London.

Häuser, C. L. 1987. The debate about the biological species concept: a review. *Z. Zool System u Evolutionsforschung* 25: 241–257.

Hengeveld, R. 1988. Mayr's ecological species criterion. *Syst. Zool.* 37: 47–55.

Hennig, W. 1966. *Phylogenetic Systematics.* Illinois University Press, Urbana, Illinois.

Hewitt, G. M. 1989. The subdivision of species by hybrid zones. Pp. 85–110 *in* D. Otte & J. A. Endler (eds.), *Speciation and Its Consequences.* Sinauer Associates, Sunderland, Massachusetts.

Key, K. H. L. 1968. The concept of stasipatric speciation. *Syst. Zool.* 17: 14–22.

Kryukov, A. P. & Blinov, V. N. 1989. [Interaction of Hooded and Carrion crows (*Corvus cornix* L. and *C. corone* L.) in the zone of sympatry and hybridization: Is there a selection against hybrids?] (In Russian, English summary.) *J. Gen. Biol.* (U.S.S.R. Acad. Sci.) 50: 128–135.

Lanyon, W. E. 1957. The comparative biology of meadowlarks (*Sturnella*) in Wisconsin. *Publ. Nuttal. Orn. Cl.* 1.

— 1962. Specific limits and distribution of meadowlarks of the desert grasslands. *Auk* 79: 183–207.

— 1966. Hybridization in meadowlarks. *Bull. Mus. Nat. Hist.* 134: 1–25.

Little, F. J., Jr. 1964. The need for a uniform system of biological nomenclature. *Syst. Zool.* 13: 191–194.

Mayr, E. 1942. *Systematics and the Origin of Species.* Columbia University Press, New York.

— 1954. Changes of genetic environment and evolution. Pp. 157–160 *in* J. S. Huxley, A. C. Hardy & E. B. Ford (eds.), *Evolution as a Process.* Allen & Unwin, London.

— 1963. *Animal Species and Evolution.* Harvard University Press, Cambridge.

— 1969. *Principles of Systematic Zoology.* McGraw-Hill, New York.

— 1982a. Speciation and macroevolution. *Evol.* 36: 1119–1132.

— 1982b. Processes of speciation in animals. Pp. 1–19 *in* D. Barigozzi (ed.), *Mechanisms of Speciation.* A. R. Liss, New York.

— 1982c. *The Growth of Biological Thought.* Harvard University Press, Cambridge.

— 1982d. Of what use are subspecies? *Auk* 99: 593–595.

— 1986. The species as category, taxon, and population. Pp. 303–319 *in* J. Rogeo & J. L. Fischer (eds.), *Histoire du Concept d'Espece dans les Sciences de la Vie.* Fondacion Singer-Polignac, Paris.

— 1988a. The why and how of species. *Biol. Philos.* 3: 431–441.

— 1988b. Recent historical developments. Pp. 32–42 *in* D. L. Hawksworth (ed.), *Prospects in Systematics.* Clarendon Press, Oxford.

Mayr, E. & Short, L. L. 1970. Species taxa of North American birds, a contribution to comparative systematics. *Publ. Nuttall. Orn. Cl.* 9.

McKittrick, M. C. & Zink, R. M. 1988. Species concepts in ornithology. *Condor* 90: 1–14.

Michener, C. D. 1964. The possible use of uninomial nomenclature to increase the stability of names in biology. *Syst. Zool.* 13: 191–194.

Nelson, G. & Platnick, N. 1981. *Systematics and Biogeography.* Columbia University Press, New York.

O'Brien, S. J. & Mayr, E. 1991. Bureaucratic mischief: recognizing endangered species and subspecies. *Sci.* 251: 1187–1188.

Paterson, H. E. 1985. The recognition concept of species. Pp. 21–29 *in* E. S. Vrba (ed.), *Species and Speciation.* Transvaal Mus. Monographs 4.

Payne, R. B. 1982. Species limits in the indigobirds (Ploceidae, *Vidua*) of West Africa: mouth mimicry, song mimicry, and description of new species. *Miscl. Publ. Mus. Zool Univ. Michigan* 162.

Payne, R. B. 1986. Bird songs and avian systematics. Pp. 87–126 *in* R. J. Johnston (ed.), *Current Ornithology* 3.

Pierce, R. J. 1984. Plumage, morphology and hybridization of New Zealand stilts *Himantopus* spp. *Notornis* 31: 106–130.

Prigogine, A. 1984. Secondary contacts in central Africa. *Proc. V. Pan-African Orn. Congr.* 81–96.

— 1985. Speciation problems with special reference to the Afrotropical region. *Mitteil. Zool. Mus. Berlin* 60: 3–27.

Raubenheimer, D. & Crowe, T. M. 1987. The recognition species concept: is it really an alternative? *So. African J. Sci.* 83: 530–534.

Ripley, S. D. 1945. Suggested terms for the interpretation of speciation phenomena. *J. Wash. Acad Sci.* 35: 337–341.

Root, R. B. 1969. Interspecific territoriality between Bewick's and House wrens. *Auk* 86: 125–127.

Rosen, D. E. 1978. Vicariant patterns and historical explanations in biogeography. *Syst. Zool.* 27: 159–188.

Short, L. L. 1969. Taxonomic aspects of avian hybridization. *Auk* 86: 84–105.

— 1971. Systematics and behavior of some North American woodpeckers, genus *Picoides* (Aves). *Bull. Am. Mus. Nat. Hist.* 145: 1–118.

— 1972. Hybridization, taxonomy and avian evolution. *Ann. Missouri Botan. Garden* 59: 447–453.

— 1982. *Woodpeckers of the World*. Delaware Mus. Nat. Hist., Monogr. Ser., 4.

Short, L. L. & Horne, J. F. M. 1985a. Aspects of duetting in some ground barbets. *Proc. V. Pan-African Orn Congr.* 729–744.

—, — 1985b. Social behavior and systematics of African barbets (Aves: Capitonidae). Pp. 255–278 *in* K.-L. Schuchmann (ed.), *Proc. Int. Symp. African Vertebrates (Bonn)*.

—, — 1988. Capitonidae: barbets and tinkerbirds. Pp. 413–486 *in* C. H. Fry, S. Keith & E. K. Urban (eds.), *The Birds of Africa*, vol. 3.

Short, L. L., Schodde, R. & Horne, J. F. M. 1983. Five-way hybridization of Varied Sittellas, *Daphaenositta chrysoptera* (Aves: Neosittidae) in central Queensland. *Austral. J. Zool.* 31: 499–516.

Sibley, C. G. 1954. Hybridization in the Red-eyed Towhees of Mexico. *Evol.* 8: 254–290.

Sibley, C. G. & L. L. Short, Jr. 1959. Hybridization in the buntings (*Passerina*) of the Great Plains. *Auk* 76: 443–463.

Sibley, C. G. & Sibley, F. C. 1964. Hybridization in the Red-eyed Towhees of Mexico: the population of the southeastern plateau region. *Auk* 81: 479–504.

Simpson, G. G. 1961. *Principles of Animal Taxonomy*. Columbia University Press, New York.

Smith, H. M. 1965. More evolutionary terms. *Syst. Zool.* 14: 57–58.

Smith, H. M. & White, F. N. 1956. A case for the trinomen. *Syst. Zool.* 5: 183–190.

Snow, D. W. (Ed.) 1978. *An Atlas of Speciation in African Non-Passerine Birds*. British Museum (Nat. Hist.), London.

— 1979. Pipridae, Cotingidae. Pp. 246–310 *in* M. A. Traylor, Jr. (ed.), *Check-list of Birds of the World*. Harvard University Press, Cambridge.

Templeton, A. R. 1989. The meaning of species and speciation: a genetic perspective. Pp. 3–27 *in* D. Otte & J. A. Endler (eds.), *Speciation and Its Consequences*. Sinauer Associates, Sunderland, Massachusetts.

Thorneycroft, H. B. 1966. Chromosomal polymorphism in the white-throated sparrow, *Zonotrichia albicollis* (Gmelin). *Sci.* 154: 1571–1572.

— 1975. A cytogenetic study of the white-throated sparrow, *Zonotrichia albicollis* (Gmelin). *Evol.* 29: 611–621.

Vande weghe, J. P. 1988. Problems in passerine speciation in Rwanda, Burundi, and adjacent areas. *Acta XIX Congr. Intern. Orn.* Pp. 2547–2552.

Van Valen, L. 1976. Ecological species, multispecies and oaks. *Taxon* 25: 233–234.

— 1978. Why not to be a cladist. *Evol. Theory* 3: 285–299.

Vrijenhoek, R. C. 1990. Genetic diversity and the ecology of asexual populations. Pp. 175–197 *in* K. Wöhrmann & S. K. Jain (eds.), *Population Biology*. Springer, Berlin and New York.

White, M. J. D. (ed.) 1978. *Modes of Speciation*. W.H.R. Freeman and Co., San Francisco.

Zink, R. M. 1988. Evolution of Brown Towhees: allozymes, morphometrics and species limits. *Condor* 90: 72–82.

Zink, R. M., Dittmann, D. L., Cardiff, S. W. & Rising, J. D. 1991. Mitochondrial DNA variation and the taxonomic status of the Large-billed Savannah Sparrow. *Condor* 93: 1016–1019.

Address: Dean Amadon & Lester L. Short, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, U.S.A.

© British Ornithologists' Club 1992

Biochemical studies of the higher level systematics of birds

by George F. Barrowclough

Received 16 April 1992

INTRODUCTION

The use of biochemical methods in avian systematics has a significantly long history, with early reports involving immunology dating back almost 100 years (e.g. Nuttall 1904); consequently, these methods are nearly as old as the *Bulletin* of the British Ornithologists' Club.

Nevertheless, the quantity of early research was minimal and the results not particularly influential until a major increase in such studies began in the 1960s. By that time the technique of protein electrophoresis had been developed sufficiently to allow rapid surveys of samples of blood and egg-white, and it quickly replaced the earlier use of serological and immunological techniques (e.g. the research programme of workers such as Erhardt 1930, Irwin & Miller 1961, Mainardi 1963 and Stallcup 1961). Rapid developments in medicine and molecular genetics were quickly integrated into research programmes in biochemical systematics. During the same period of time, advances in analytical methods, along with philosophical insights into the nature of phylogenetic inferences, had resulted in rapid changes in systematic practice. Thus, the advances in biochemical technology and analysis used in avian taxonomy during the past 30 years, reviewed here, have been remarkable. The earlier, largely immunological work on avian systematics was reviewed previously by Sibley *et al.* (1974).

In considering the achievements of biochemical systematics, important distinctions arise concerning the taxonomic level of the problem. Microtaxonomic or microevolutionary studies are inquiries which are aimed at elucidating the genetic structure of populations and problems of the origin of species; whereas macrotaxonomy is the study of the relatedness and phylogeny of species and higher taxa. Until now, the success of molecular methods at these 2 levels has differed considerably. The quality and impact of biochemical studies of macrotaxonomy are the subjects of this review. Biochemical studies of microevolution in birds were the subject of earlier reports (Barrowclough 1983, Evans 1987).

THE ELECTROPHORESIS ERA

General proteins

Some electrophoretic experiments on avian proteins were reported as early as the 1930s (Landsteiner *et al.* 1938); however, McCabe & Deutsch (1952) reported on comparative electrophoretic mobility of egg-white proteins from 37 species representing several orders of birds, and it was this work that led Sibley, his graduate students and post-doctoral associates to begin a major research programme in electrophoresis, principally aimed at elucidating higher level avian relationships. The work involved first paper, and later starch-gel electrophoresis of egg-white proteins followed by treatment with a general protein stain. Additional studies involved haemoglobins, and blood plasma proteins, eye lens proteins, and feather keratins. The utility of the technique lies in the detection of mobility differences among proteins based on their electrical charge and the shape of the molecule; thus, similarities and differences among taxa are documented. Two major monographs (Sibley 1970, Sibley & Ahlquist 1972) summarized many of these results.

Statements about the Sturnidae are typical of the results reported in these works. For example, egg-white electrophoretic patterns of 10 species of starlings in 7 genera are cited in the passerine volume; the patterns of *Sturnus* and *Lamprotornis* were found to differ in a major component protein and those of *Sturnus* and the woodswallow *Artamus* appeared to match well. Thus, Sibley was able to conclude, among other things, that the first 2 genera may not be closely related and that the Artamidae are one of the most likely relatives of the Sturnidae.

Techniques for separation of proteins became more sophisticated in the latter 1960s and early 1970s and, at least in Sibley's laboratory, starch-gel methods were replaced by acrylamide gels and then isoelectric focusing in acrylamide. The amount of energy, resources and talent that went into this research, in a number of laboratories, over 2 decades was enormous; the quantity of data produced was voluminous. Moreover, the problems addressed were of genuine taxonomic interest. Unfortunately, however, it is clear in retrospect that this research programme produced few lasting accomplishments. This was due to 2 factors: the absence of quantitative methods of analysis and insufficient informative characters. Neither of these problems was understood by the systematics community at the time of the work, nor was the failure peculiar to one research programme.

It is now generally recognized that in order to infer a phylogeny, it is necessary to use cladistic or other phylogenetic methods that can distinguish between derived and primitive similarity (e.g. Wiley 1981). This recognition only became widespread in the 1970s, after much of the general protein work had been eclipsed by newer techniques. In principle, phylogenetic methods could have been applied to egg-white and other studies of proteins. For example, if homology of specific proteins on the gels could be established from species to species—a serious problem with total protein staining methods—alternate mobilities could be treated as alternate character states and analysed in a phylogenetic framework. In fact, this line of reasoning later was pursued by workers such as Brush & Witt (1983) and Knox (1980).

For example, in a study of the relationships of several species of Pelecaniform birds, Brush & Witt determined the electrophoretic mobility of feather keratins under several pH conditions; they computed genetic distances among the taxa, based on the sharing of bands among species, using general protein staining. Phylogenetic trees were computed based on the genetic distances. The trees were generally similar in that congeneric species tended to stay together, but the precise branching patterns depended on both the pH of the electrophoretic experiments and

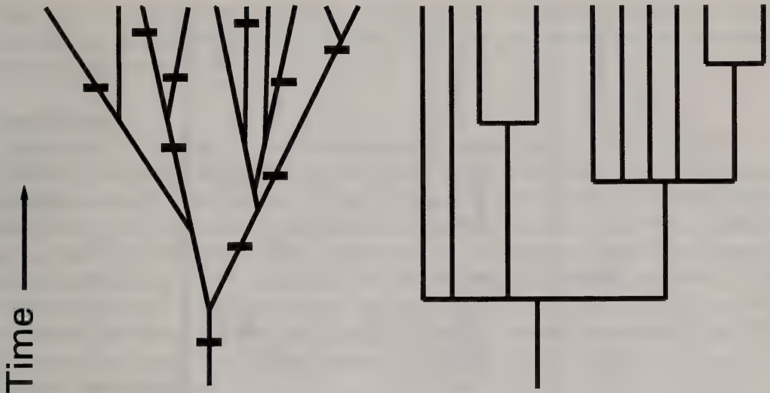


Figure 1. The details of evolutionary branching patterns cannot be recovered given too few characters or when branching events are too close in time. Left: Hypothetical evolutionary tree for 10 species with 10 character changes, randomly distributed in time, indicated by bars. Right: Maximally informative tree that can be inferred from character data shown on left.

the algorithm used to infer the tree. Such results indicate the dependence of pattern identity on pH and the sensitivity of tree topology to assumptions in the algorithms about constancy of rates of evolution.

The second serious problem with the general protein approach was the number of characters available for analysis. In a starch-gel, egg-white studies might indicate a half dozen or so easily visualized proteins. For avian haemoglobins, the number is less. If one's objective is to work out a fully resolved phylogeny for the taxa of interest (i.e. no nodes of the tree generating more than 2 lineages), then there must be at least one mobility change in one character between every pair of nodes of the actual tree (Fig. 1). Consequently, there must be more total character states in the data set than there are taxa in the study. Moreover, if the amount of evolutionary time between nodes of the actual tree was short for some of the branches, then the probability of a character state change for that branch is also small. Therefore, a large number of characters are necessary for there to be a significant chance of a change occurring along the short branches (e.g. see Lanyon 1988). For electrophoresis of egg-white, the number of potential character states is insufficient to produce a fully resolved phylogenetic tree for more than a few taxa (Table 1). With isoelectric focusing, the number of distinguishable proteins and mobility states increases, but then homology problems also are accentuated.

Once these 2 major problems are acknowledged, it is apparent that either many more characters must be made available in order to attack the major problems of higher level systematics (for example, the relationships of the families of birds) or one must be content with lesser goals: identifying clades rather than working out fully resolved trees or allocating a taxon of dubious affinities to one of several suspected groups. It was at this reduced level of resolution that egg-white studies achieved some limited success. For example, Sibley (1968) was able to show that

TABLE 1

Approximate time, in PhD project equivalents during decade when technique was in vogue, to solve major problems in avian systematics using various biochemical techniques

Nature of Problem	General Protein Electro-phoresis	Allozyme Electro-phoresis	Micro-complement Fixation	Peptide Mapping	Amino Acid Sequencing	DNA-DNA Hybridization	Restriction Enzymes	DNA Sequencing
Allocate a problematical species to 1 of 5 families:	1	1	1	1	5	1	1	1
Resolve relationships of 25 species in a family:	IC	1 (IC?)	1	1 (IC?)	25	1	1	1
Resolve relationships among single representatives of each of 175 families of birds:	IC	IC	50	IC	175	50	7 (IC?)	7
Complexity of technique:	N	N	N^2	N	N	N^2	N	N

Notes. IC = Technique not capable of resolving problem due to insufficient characters.
N = number of taxa.

Zeledonia belonged somewhere in the New World 9-primaried oscine assemblage rather than with either the wrens or thrushes, as previously had been thought.

Allozymes

Lewontin & Hubby (1966) introduced the technique of electrophoresis followed by specific enzyme staining to a general audience of evolutionary biologists and systematists. This represented a major breakthrough: it made many more characters available than previously and was a relatively inexpensive technique. The ability to examine the mobility states of single enzymes greatly reduced the homology problem present in total protein staining. Furthermore, the number of different enzyme stains developed for medical clinicians and human geneticists meant that 30 or 40 characters were available, some of which might show 3, 4 or more different mobilities.

By the late 1970s and early 1980s a substantial number of workers in avian systematics were using allozyme techniques. Initially much of this research involved somewhat higher level systematics, for example, working out the relationships of species within genera and genera within families (e.g. Barrowclough & Corbin 1978, Avise *et al.* 1982, Gutiérrez *et al.* 1983). However, the quantity of this work was soon superseded by studies of intraspecific variation, for example, hybrid zones (e.g. Barrowclough 1980, Corbin *et al.* 1979), differentiation among introduced populations (e.g. Baker & Moeed 1987), differentiation among vocal dialects (e.g. Baker 1982), and variation among variable taxa that might represent either species or subspecies (e.g. Zink 1988, Johnson & Marten 1988). These studies of intraspecific variation did have major impact on avian systematics in the broad sense: in North America they led to changes in opinion about species status of a number of taxa (e.g. see Johnson & Marten 1988). More generally, they led to a general interest in avian evolutionary genetics and a more quantitative understanding of the population genetic structure of birds (Rockwell & Barrowclough 1987). The impact of the higher level studies, however, was considerably less.

Early on in the allozyme research enterprise it became clear that there was considerable heterogeneity in the degree of variability and rates of differentiation among the various genetic loci routinely analysed with allozyme electrophoresis (e.g see Evans 1987). Thus, although it might appear that 40 loci and 100 or more alleles were available for studies of higher level relationships, in fact this was a major overestimate. Some loci, for example the malate dehydrogenases, were so uniform that little variation was detected at the level of orders of birds; such loci were consequently of little value for studies of phylogeny within families or genera. Other loci, for example the non-specific esterases and adenosine deaminase, varied so much that they were useless for studies much above the species level—so many alleles were present that results were dominated by alleles unique to each taxon (autopomorphy) and convergences (homoplasy) rather than shared derived mobility states (synapomorphy). Consequently, at any given taxonomic level, the number of informative character states was often quite small and true cladistic studies produced polychotomies—unresolved phylogenies—because there were no character states defining many of the possible nodes. This was the same limitation found in the earlier studies involving general protein staining.

A second major problem with many allozyme studies at higher levels was a general failure of investigators to take on real taxonomic problems. In the late 1970s, when the techniques first became available, a smattering of general studies was perhaps justified in order to determine the usefulness of the technique, the level at which it was useful, etc. Unfortunately, however, the allozyme work never matured to the point where workers consistently investigated problems such as phylogeny of all or even the major part of a taxon. Thus, one might find a study of a few thrushes representing a small fraction of a taxonomic problem. Studies such as Gerwin & Zink's (1989) phylogeny of 8 of the 9 species of hummingbirds in the genus *Heliodoxa* were in a minority. At higher taxonomic levels even less was done; thus, the taxonomic awareness and intensity found in Sibley's earlier work with general protein staining was not generally present in researchers using the newer technique. In the cases in which researchers pushed the technique in useful directions, some interesting results were produced. Kitto & Wilson (1966), for example, found that one allele at the mitochondrial MDH locus defined the order Charadriiformes and a second allele identified the major clade of swifts plus hummingbirds. Likewise, Matson (1989) found the expression of a testes-specific lactate dehydrogenase that was a synapomorphy for Columbiformes. Such limited, but useful, results were, in retrospect, about all that should have been expected from the technique at the familial and ordinal levels.

Allozyme electrophoresis had its lasting impact at lower taxonomic levels. First, the potential at higher levels was not widely appreciated and pursued and, second, given that the number of potential character states was always destined to be small at any taxonomic level, fully resolved phylogenetic trees were not really a possibility. The few interesting results that were achieved at higher levels did not have major influence on practical systematics; the results were often not new, the taxonomic sampling was too restricted, or the results were ambiguous. For example, Johnson *et al.* (1988) examined most of the species in the family Vireonidae using allozyme electrophoresis. Their results indicated long, separate, evolutionary histories for several lineages of these birds; however, the detailed phylogenetic relationships inferred for the taxa varied depending upon the algorithm used to analyze the data. Thus, many of the details necessary to produce a new taxonomic treatment of the family remained ambiguous.

OTHER PROTEIN TECHNIQUES

Microcomplement fixation

The immunological response of an organism to an antigen is based on many aspects of both the composition and conformational structure of the molecule *in vivo*. Thus, although the biochemical nature of the reaction itself is still the subject of intense investigation, it is nevertheless clear that more information is being assayed than just charge and size, as in electrophoresis. Less information is available than in direct amino acid sequencing of the protein, but the cost is a fraction of that technique. Consequently, microcomplement fixation was used in a few labs for a decade or so in the late 1970s and the 1980s. This method allowed one to obtain a quantitative measure of the similarity of proteins based on the immunological response of the antibodies produced against a protein from one taxon on the homologous protein of the other taxon.

The major limitation of the method is that the technique of necessity yields information on the overall immunological distance between 2 organisms for a given protein; individual character information is not available. Thus, any phylogenetic analysis would require distance methods. These are less reliable than character methods because of their inability to identify specific apomorphies and homoplasies and, unless one assumes the protein evolves in a clocklike fashion, at the very least immunological experiments must be performed on all combinations of taxa; that is, a complete matrix of information is required. This makes the technique more and more expensive as the number of taxa, N, increases because the number of requisite experiments becomes of the order of N^2. Consequently, the technique would be most useful for working out relationships of a few species or allocating a species of unknown affinities to one of two or three higher taxa. For an investigator working out the relationships of approximately 175 avian families, other techniques would make more economic sense and ultimately involve less time.

Allan Wilson and his associates worked with the technique for approximately 15 years. In this period of time they used 4 major proteins (albumin, lysozyme, ovalbumin and transferrin) and addressed problems at several levels in a number of avian groups. Of particular interest to Wilson were the galliform birds; in part this was due to the availability of substantial quantities of proteins for birds frequently kept in aviaries. However, in spite of the effort directed at the problem, the results that could be obtained were restricted by the necessity to do reciprocal experiments, obtain a complete N × N matrix of data, and confirm results with alternate proteins. For example, Prager & Wilson (1976) reported on a study of 24 species from 4 families of galliforms and 1 and 2 representatives each of 13 other orders of birds. The resulting phylogenetic tree (based on a distance analysis) was surprisingly similar to some recent results of Sibley & Ahlquist (1990); nevertheless, the sparsity of the taxonomic sampling, the publication in a non-ornithological journal, and the inconsistencies with the then current ideas about relationships, led to the paper having little impact on avian systematic thought.

Peptide mapping

Electrophoretic experiments are capable of separating homologous proteins that differ in charge, isoelectric point and, to a lesser extent, shape. Nevertheless, it was recognised that 2 proteins with identical electrophoretic mobility could still vary in amino acid sequence. Before amino acid sequencing became available, information on sequence differences could only be obtained by indirect methods. One briefly popular technique was to cleave a purified protein into peptides with enzymes having highly specific activity (e.g. trypsin) and then compare the resulting peptides using electrophoresis and chromatography. Although a substantial number of characters can be obtained per protein with this method (20 or more for ovalbumins), establishing homology of the individual peptides can be a difficult problem. In addition, the technique is time-consuming and expensive; it never became very popular. Of the little published work, the best such study was Corbin's (1968) work on pigeons of the genus *Columba*; however, that analysis predates the adoption of modern phylogenetic methods. Thus, his results were summarized in statements concerning the degree of similarity of taxa rather than as a phylogenetic tree.

Peptide mapping, like all the techniques listed thus far, involves an indirect method for revealing character differences resulting from amino acid sequence differences. By the mid-1960s it had become possible, albeit laborious, to obtain the actual amino acid sequence.

Amino acid sequencing

A large protein may consist of a string of as many as several hundred amino acids, each of which can take on, in theory, one of 20 states. Thus, the sequence data for just a few proteins has the potential to yield a vast quantity of systematic data. Moreover, by the time amino acid sequences began to appear in numbers in the mid-1970s, numerical phylogenetic techniques were also becoming available. Consequently, by picking proteins evolving at an appropriate rate, investigators might have used this technique to solve most of the major problems in higher level avian systematics. Many researchers realized this, but the technique never became labour or cost effective. Allan Wilson mentioned (pers. comm.) in 1977 that he thought sequencing the lysozyme of a single species was a good Ph.D. project. Thus, given approximately 175 families of birds and 2000 genera, the higher level systematics of birds might have been worked out in a few generations of researchers (see Table 1).

In fact, however, amino acid sequences were worked out only for a small number of taxa for a few proteins because the Wilson lab at the University of California at Berkeley was the sole major proponent of the technique among avian systematists. For example, one report from Wilson's lab (Jolles *et al.* 1979), reported lysozyme sequences for 9 species of birds; a chachalaca (Cracidae) was found to be quite distant in its sequence from other galliforms, including a guineafowl. Biochemical physiologists also sequenced a number of avian globin genes, but those data were never synthesized and brought to the attention of avian workers. The amino acid sequence data eventually produced were too few to have a real effect on avian systematics.

THE DNA ERA

All protein methods, including amino-acid sequencing, are unable to reveal some potentially useful character state data because proteins are translated from DNA sequences that contain more information than do the corresponding amino acid sequences. For example, the 2 DNA sequences TTA and CTG both code for the same amino acid, leucine. If 2 taxa of birds had these alternate sequences, protein techniques would fail to detect the differences. In theory, then, studies of DNA offer the potential for more characters, hence a greater chance of finding state changes along short branches, thus more resolution, etc. All protein methods can be viewed, in fact, as indirect attempts to get at DNA sequence information. As soon as the relationship between DNA sequences and protein coding was understood in the 1950s, it was realized that DNA analysis would be the ultimate tool of molecular systematics. However, DNA sequencing was preceeded by less direct techniques for developing this rich source of information.

DNA-DNA hybridization

Shields & Strauss (1975) first reported on the application of a method for comparing the overall DNAs of species in their study of some New World finches. In this method an index to the similarity of the DNAs of a pair of species is found by monitoring the melting temperature of hybrid molecules of DNA formed in the laboratory. In general the more similar 2 DNA sequences, the higher the melting point; this can be precisely measured under controlled conditions. A general review of the technique can be found in Sibley & Ahlquist (1990). The approach was adopted by Sibley and his colleagues in the early 1970s and a major research programme undertaken that has ultimately involved comparisons of thousands of individuals of hundreds of species.

The results of this research have been quite controversial, largely because of concerns about the method of analysis of the data. Besides problems of data reduction peculiar to the Sibley & Ahlquist laboratory (Lanyon 1992), the method itself inevitably produces only a measure of the overall distance between 2 taxa. Thus, there are no character data to analyze; consequently, methods of phylogenetic analysis that are free of assumptions about evolutionary rates ought to be used and these necessitate a complete matrix of intertaxon distances. Once again this causes the amount of work involved to increase as the square of the number of taxa. For practical reasons, then, DNA-DNA hybridization studies must involve a small number of taxa or involve dubious assumptions about evolutionary rates. The advantage of the technique was that it does examine DNA; hence in the 1980s it represented a novel dataset, and it involves a large part of the total genome, not just a single gene or class of genes (e.g. enzymes). However, contrary to statements of some proponents, the latter advantage does not entirely vitiate problems of rate differences. It was argued (e.g. Sibley & Ahlquist 1983) that, because a very large number of genes were being analyzed, rate differences among genes would average out to a grand mean and produce an overall constant rate of evolutionary change. This would make the data easier to collect and analyze because a complete data matrix is not always essential for clocklike distances. It is true that the law of large numbers works to the technique's advantage for one of the sources of variation—average differences in evolutionary rates among genes within individuals. However, other sources of variation are not affected by this averaging; these include changes in rates of substitution across the entire genome due to: 1.) demographic events, such as fluctuating population sizes; 2.) relative efficacy of DNA repair mechanisms in alternate lineages; 3.) differing mutation or fixation rates in taxa with differing life histories or generation times. Thus, a clocklike pattern of evolutionary change is an empirical issue, to be demonstrated, not postulated.

To date, the best study using DNA hybridization in birds was Sheldon's (1987) analysis of the herons (Ardeidae). About half of the total species were treated, but only 13 of the herons were included in a complete data matrix. In part this was because each pair of species was replicated 10 times. Nevertheless, the study was more complete than many biochemical studies in that all the major lineages were represented; thus the results were of real interest to systematists. However, the study indicates something of the limitations of the technique. The necessity to replicate a complete data matrix several times in order to determine the relationships of the major lineages of a moderate sized family took a considerable amount of time and effort. This study is near the upper limit of a reasonably sized investigation using DNA-DNA hybridization; it comprised Sheldon's Ph.D research.

Bledsoe's (1988) DNA-DNA study of 9-primaried oscines was also a Ph.D. project. It involved a complete 13 x 13 matrix of taxa. Of necessity, however, only a few genera of this very large assemblage could be included; thus, the results do not have immediate effect on the details of avian taxonomy. Rather, they suggest interesting problems to follow up. The same might be said of the massive data produced by Sibley & Ahlquist. Because of the widespread concerns about the details of the analysis, the lack of complete data matrices for most of the published material, and concerns about distances data in general, there is scepticism in the systematics community about the interpretation of these data (e.g. Cracraft 1987, Gill & Sheldon 1991, Lanyon 1992). It is unlikely much can be done about this, however; producing a complete data matrix for 175 avian families is not feasible with the technique. Unquestionably some of Sibley & Ahlquist's suggestions will be confirmed by future studies; but ornithologists will look to other techniques for support for these hypotheses.

Restriction enzymes

Genetic discoveries in the 1970s and 1980s made available a battery of enzymes that cleave specific sequences of DNA; for example, the restriction enzyme EcoR1 only cuts the sequence GAATTC. In a large sequence of DNA, such 'recognition sites' will occur at a particular position in some taxa and, due to evolutionary changes, not in others. With a large enough number of these enzymes and a sufficiently long sequence of DNA, a large number of character states—the cleaved sites—will be available for analysis.

An appreciable amount of research using this technique has been underway for only about 5 years. In practice, most workers have used mitochondrial DNA in order to reduce the number of sites to a reasonable number (nuclear DNA is so extensive that a large number of recognition sites invariably are found; the resulting number of fragments visualized on a gel is so great that homology becomes a problem). Analyzed cladistically, such data, if sufficient in number, can yield fully resolved branching diagrams for problems of taxonomic interest. Relatively expensive, the technique has been used only in a few labs; it is so recent that much of the work to date has consisted of exploratory studies aimed at determining the usefulness of the method at various taxonomic levels (e.g. Avise & Zink 1988). A major impact on avian systematics is only beginning to be felt (e.g. Zink & Dittmann 1991, Gill & Slikas 1992). However, the technique is already being superseded by a newly available method for direct sequencing of DNA.

DNA sequences

Until a few years ago, actual sequencing of DNA was an expensive, elaborate procedure involving genetic cloning in vectors, etc. However, the development of the polymerase chain reaction (PCR) for gene amplification and rapid and efficient sequencing technology has now made it possible to produce large quantities of specific sequences of DNA from relatively large numbers of individuals in a reasonable period of time. Thus, it is already feasible to perform a phylogenetic study involving the DNA sequence of more than 900 base pairs for more than 20 taxa (e.g. Richman & Price 1992). If even 10% or 20% of such bases are variable, then an appreciable amount of information will be available for phylogenetic inference. Because each new sequence can be compared with all previous ones, for the same gene, the amount of work required in a study increases only as the number of species, N. The potential of this technique is such that it is rapidly being adopted by avian systematists throughout the world.

At present only a few genes are being sequenced; the most widely used is the mitochondrial cytochrome-b gene. Various domains of this gene appear to evolve at different rates—reflecting the functional constraints of alternate portions of the translated protein. The gene has already proved useful for systematics and ecological problems; for example, using cytochrome-b sequences, Richman & Price (1992) were able to produce a fully resolved (completely dichotomous tree) phylogeny for 22 species of sylviid warblers. They then used the tree to interpret patterns of morphological variation among 8 species of *Phylloscopus* warblers sympatric in the Himalayas.

Various other genes, mitochondrial and nuclear, are known to have greater (D-loop, ATPase8) and lesser (cytochrome-c oxidase) rates of evolution than cytochrome-b (Arctander 1991). It is feasible to choose such alternate genes, with their varying rates of nucleotide substitution, as a function of the taxonomic problem of interest. Thus, the technology is essentially available today to produce voluminous data on avian relationships at many levels—from populations within species, to species within genera, to families within orders (e.g. Birt-Friesen *et al.* 1992, Johnson & Cicero 1991, Edwards *et al.* 1991). The number of characters potentially available is not likely to be limiting except for vanishingly short branches. Numerical algorithms to deal with the quantity of data in a phylogenetic manner are more of a problem, but computer power is rapidly improving. It does not take great bravery to predict that a decade from now many of the major problems of avian systematics, and certainly the relationships of the families, will be solved using this technique.

Conclusions

The past century has seen a growing amount of research in the higher level systematics of birds using biochemical techniques, but particularly, and rapidly, over the past 30 years. Up to the present time, however, the results have not lived up to expectations, and it is only in recent years that a sufficient understanding of the various problems have emerged. In particular, results have been limited due to an absence of analytical method, a lack of sufficient numbers of characters, and, more recently, a failure to work on genuine systematic problems.

In Table 1, the efficacies of 8 major biochemical techniques are evaluated in terms of 3 typical problems in avian systematics. I have taken as the basis for comparison the doctoral dissertation project as the unit of time; this is convenient as many results have been obtained through such projects, providing a natural standardization; expense might have been an alternative. The simplest problem considered is the allocation of a difficult species to a family of birds; for example, what are the affinities of the Hoatzin, *Opisthocomus*? Second, what is the phylogeny of the species in a large genus or a small family, e.g. the Alcidae? Third, is the dominant problem of avian higher level systematics the relationships among avian families? Thus, for example, electrophoresis with general protein staining, intensively used in the 1960s, yielded too few characters and pre-dated quantitative analytical methods of phylogenetic inference; in retrospect this and other techniques were inappropriate for resolving many of the problems on which they were used. This same limitation was more or less true of allozyme work. Microcomplement fixation, an immunological technique, and amino acid sequencing were the first techniques available that were at all appropriate for the highest level avian systematics, but both had real limitations. Amino acid sequences were too time consuming and expensive to obtain. The immunological technique, while useful at the level of intrafamilial relationships, has N^2 complexity. Consequently, a problem involving 175 species is 7^2 times as difficult as a problem with 25 species. The recently used technique of DNA-DNA hybridization has the same complexity.

During the 1970s and 1980s, many workers in avian systematics shifted away from macrotaxonomy questions to the study of microevolutionary processes; in part this may have been due to the failure or expense of previous techniques. However, the long sought goal of molecular systematics, DNA sequences, has become feasible in the past 5 years. The technique offers access to numerous characters useful at all taxonomic levels, and algorithms for data analysis are becoming widely available. For the first time (Table 1), a technique is available that is appropriate and economical for solving the major problem in avian systematics, the relationships of the families of birds.

Acknowledgements

I am grateful to C. Griffiths, J. Groth and P. Sweet for helpful comments on this manuscript, and to P. Sweet for the preparation of Fig. 1.

References:

Arctander, P. 1991. Avian systematics by sequence analysis of mtDNA. *Proc. Intl. Ornithol. Conr.* 20: 619–628.

Avise, J. C., Aquadro, C. F. & Patton, J. C. 1982. Evolutionary genetics of birds. V. Genetic distances within Mimidae (mimic thrushes) and Vireonidae (vireos). *Biochem. Genet.* 20: 95–104.

Avise, J. C. & Zink, R. M. 1988. Molecular genetic divergence between avian sibling species: King and Clapper Rails, Long-billed and Short-billed Dowitchers, Boat-tailed and Great-tailed Grackles, and Tufted and Black-crested Titmice. *Auk* 105: 516–528.

Baker, A. J. & Moeed, A. 1987. Rapid genetic differentiation and founder effects in colonizing populations of common mynas *(Acridotheres tristis)*. *Evolution* 41: 525–538.

Baker, M. C. 1982. Vocal dialect recognition and population genetic sequences. *Amer. Zool.* 22: 561–569.

Barrowclough, G. F. 1980. Genetic and phenotypic differentiation in a wood warbler (genus *Dendroica*) hybrid zone. *Auk* 97: 655-668.

— 1983. Biochemical studies of microevolutionary processes. Pp. 223-261 *in* A. H. Brush & G. A. Clark, Jr. (eds), *Perspectives in Ornithology*. Cambridge Univ. Press, New York.

Barrowclough, G. F. & Corbin, K. W. 1978. Genetic variation and differentiation in the Parulidae. *Auk* 95: 691–702.

Birt-Friesen, V. L., Montevecchi, W. A., Gaston, A. J. & Davidson, W. S. 1992. Genetic structure of thick-billed murre (*Uria lomvia*) populations examined using direct sequence analysis of amplified DNA. *Evolution* 46: 267–272.

Bledsoe, A. H. 1988. Nuclear DNA evolution and phylogeny of the New World nine-primaried oscines. *Auk* 105: 504–515.

Brush, A. H. & Witt, H.-H. 1983. Intraordinal relationships of the Pelecaniformes and Cuculiformes: electrophoresis of feather keratins. *Ibis* 125: 181–199.

Corbin, K. W. 1968. Taxonomic relationships of some *Columba* species. *Condor* 70: 1–13.

Corbin, K. W., Sibley, C. G. & Ferguson, A. 1979. Genic changes associated with the establishment of sympatry in orioles of the genus *Icterus*. *Evolution* 33: 624–633.

Cracraft, J. 1987. DNA hybridization and avian phylogenetics. *Evol. Biol.* 21: 47–96.

Edwards, S. V., Arctander, P. & Wilson, A. C. 1991. Mitochondrial resolution of a deep branch in the genealogical tree for perching birds. *Proc. Roy. Soc. Lond. B.* 243: 99–107.

Erhardt, A. 1930. Die serodiagnostischen untersuchungen in der ornithologie. *J. Ornithol.* 78: 214–234.

Evans, P. G. H. 1987. Electrophoretic variability of gene products. Pp. 105–162 *in* F. Cooke & P. A. Buckley (eds), *Avian Genetics*. Academic Press, London.

Gerwin, J. A. & Zink, R. M. 1989. Phylogenetic patterns in the genus *Heliodoxa* (Aves: Trochilidae): an allozymic perspective. *Wilson Bull.* 101: 525–544.

Gill, F. B. & Sheldon, F. H. 1991. The birds reclassified. *Science* 252: 1003–1005.

Gill, F. B. & Slikas, B. 1992. Patterns of mitochondrial DNA divergence in North American crested titmice. *Condor* 94: 20–28.

Gutiérrez, R. J., Zink, R. M. & Yang, S. Y. 1983. Genic variation, systematic, and biogeographic relationships of some galliform birds. *Auk* 100: 33–47.

Irwin, M. R. & Miller, W. J. 1961. Interrelationships and evolutionary patterns of cellular antigens in Columbidae. *Evolution* 15: 30–43.

Johnson, N. K. & Cicero, C. 1991. Mitochondrial DNA sequence variability in two species of sparrows of the genus *Amphispiza*. *Proc. Intl. Ornithol. Congr.* 20: 600–609.

Johnson, N. K. & Marten, J. A. 1988. Evolutionary genetics of flycatchers. II Differentiation in the *Empidonax difficilis* complex. *Auk* 105: 177–191.

Johnson, N. K., Zink, R. M. & Marten, J. A. 1988. Genetic evidence for relationships in the avian family Vireonidae. *Condor* 90: 428–445.

Jolles, J., Ibrahimi, I. M., Prager, E. M., Schoentgen, F., Jolles, P. & Wilson, A. C. 1979. Amino acid sequence of pheasant lysozyme. Evolutionary change affecting processing of prelysozyme. *Biochemistry* 13: 2744–2752.

Kitto, G. B. & Wilson, A. C. 1966. Evolution of malate dehydrogenase in birds. *Science* 153: 1408–1410.

Knox, A. G. 1980. Feather protein as a source of avian taxonomic information. *Comp. Biochem. Physiol.* 65B: 45–54.

Landsteiner, K., Longsworth, L. G. & van der Scheer, J. 1938. Electrophoresis experiments with egg albumins and hemoglobins. *Science* 88: 83–85.

Lanyon, S. M. 1988. The stochastic mode of molecular evolution: what consequences for systematic investigations? *Auk* 105: 565–573.

Lanyon, S. M. 1992. [*Review of*] *Phylogeny and Classification of Birds. A Study in Molecular Evolution* by C. G. Sibley & J. E. Ahlquist. *Condor* 94: 304–307.

Lewontin, R. C. & Hubby, J. L. 1966. A molecular approach to the study of genetic heterozygosity in natural populations. II. Amount of variation and degree of heterozygosity in natural populations of *Drosophila pseudoobscura. Genetics* 54: 595–609.

Mainardi, D. 1963. Immunological distances and phylogenetic relationships in birds. *Proc. Intl. Ornithol. Congr.* 13: 103–114.

Matson, R. H. 1989. Distribution of the testis-specific LDH-X among avian taxa with comments on the evolution of the LDH gene family. *Syst. Zool.* 38: 106–115.

McCabe, R. A. & Deutsch, H. F. 1952. The relationships of certain birds as indicated by their egg white proteins. *Auk* 69: 1–18.

Nuttall, G. H. F. 1904. *Blood Immunity and Blood Relationship*. Cambridge University Press, Cambridge.

Prager, E. M. & Wilson, A. C. 1976. Congruency of phylogenies derived from different proteins. *J. Mol. Evol.* 9: 45–57.

Richman, A. D. & Price, T. 1992. Evolution of ecological differences in the Old World leaf warblers. *Nature* 355: 817–821.

Rockwell, R. F. & Barrowclough, G. F. 1987. Gene flow and the genetic structure of populations. Pp. 223–255 *in* F. Cooke & P. A. Buckley (eds), *Avian Genetics*. Academic Press, London.

Sheldon, F. H. 1987. Phylogeny of herons estimated from DNA-DNA hybridization data. *Auk* 104: 97-108.

Shields, G. F. & Straus, N. A. 1975. DNA-DNA hybridization studies of birds. *Evolution* 29: 159–166.

Sibley, C. G. 1968. The relationships of the "wren-thrush", *Zeledonia coronata* Ridgway. *Postilla* 125: 1–12.

— 1970. A comparative study of the egg-white proteins of passerine birds. *Bull. Peabody Mus. Nat. Hist.* 32: 1–131.

Sibley, C. G. & Ahlquist, J. E. 1972. A comparative study of the egg-white proteins of non-passerine birds. *Bull. Peabody Mus. Nat. Hist.* 39: 1–276.

Sibley, C. G. & Ahlquist, J. E. 1983. Phylogeny and classification of birds based on the data of DNA-DNA hybridization. *Curr. Ornithol.* 1: 245–292.

—, — 1990. *Phylogeny and Classification of Birds*. Yale University Press, New Haven.

Sibley, C. G., Corbin, K. W., Ahlquist, J. E. & Ferguson, A. 1974. Birds. Pp. 89–176 *in* C. A. Wright (ed), *Biochemical and Immunological Taxonomy of Animals*. Academic Press, London.

Stallcup, W. B. 1961. Relationships of some families of the suborder Passeres (songbirds) as indicated by comparisons of tissue proteins. *J. Grad. Res. Ctr. S. Meth. Univ.* 29: 43–65.

Wiley, E. O. 1981. *Phylogenetics*. J. Wiley & Sons, New York.

Zink, R. M. 1988. Evolution of Brown Towhees: allozymes, morphometrics and species limits. *Condor* 90: 72–82.

Zink, R. M. & Dittmann, D. L. 1991. Evolution of Brown Towhees: Mitochondrial DNA evidence. *Condor* 93: 98–105.

Address: G. F. Barrowclough, Department of Ornithology, American Museum of Natural History, New York, NY 10024, U.S.A.

© British Ornithologists' Club 1992

Methodology in avian macrosystematics

by Walter J. Bock

Received 9 March 1992

Introduction

Interest in avian macrosystematics has a history that extends for over 200 years from the early beginnings of systematics. Analysis of this history is in itself a most interesting subject as the advances made over the past 200 years have been irregular and plagued with pitfalls, stops and starts, with periods of great activity interspersed with little to no work. An adequate historical review of avian macrosystematics does not exist, but cannot be undertaken here.

Macrosystematics includes 2 separate and quite different explanatory systems, with distinct modes of group hypotheses and disparate patterns of testing against secondary hypotheses and finally against empirical observations (Bock 1973: 391, 1977, 1981). These are: (a) explanations about the evolutionary relationships of organisms expressed in systems of biological classification; and (b) explanations about the pattern of phylogenetic branching expressed in a phylogenetic diagram. In both explanatory modes, groups of organisms are recognized, but the nature of these groups differ sharply from one another (see below). To be complete, the findings of any macrosystematic analysis should be expressed both in a biological classification and in a phylogenetic diagram, each of which provides different types of information about the organisms. Many systematists, e.g. cladists, argue that these 2 modes of explanation represent the same information; consequently, cladistic classifications are redundant with diagrams of phylogenetic branching. This approach is rejected by evolutionary systematists as lacking important information contained in evolutionary classifications. Both modes of explanation are equally important, but here I limit my discussion to the formulation and testing of biological classifications, with the clear realization that this is only one part of avian macrosystematics.

During the past 200 years, considerable advance has been achieved in recognizing many of the major groups of birds (orders and families), although considerably less understanding has been reached in clarifying the relationships of these groups to each other. Many, indeed most, of the groups we recognize today, such as waterfowl (Anatidae), pigeons (Columbidae), parrots (Psittaciformes), woodpeckers (Picidae), among many others, are accepted by all ornithologists. In this way, some natural groups of birds can be said to be robust, that is, recognized by all workers regardless of their approach to systematics, or which characters are used in the analysis, and how well or poorly the characters have been analyzed. Pigeons are pigeons, parrots are parrots, gulls are gulls, owls are owls. Even the novice in avian systematics will assign species correctly to these robust groups. The real test of our understanding of avian macrosystematics—especially our comprehension of the methodology used to formulate and especially to test, classifications—comes with the many unresolved general systematic problems in birds, such as: what are the relationships of the Hoatzin (*Opisthocomus*)?; are the Piciformes a natural group?; are the palaeognathous birds and the ratites monophyletic groups?; what are the relationships of the Pteroclidae?; or of the Coliidae?; or of the Trogonidae?; or of the Cathartidae?; or of many families of oscine birds within this suborder? It is naive to claim that even the best methodology will solve all taxonomic problems as some avian groups may prove stubbornly resistant to the best attempts to resolve their relationships.

The past 40 years have proven to be a period of exceptionally high activity in avian macrosystematics, following a half century of sluggishness. During these 40 years, greatest emphasis has been placed on the discovery of new taxonomic features to supplement traditional morphological features used for the previous 150 years. Initially, considerable emphasis was given to behavioural features, but this interest was short lived. Subsequently, more and more attention was given to chemical features, such as egg-white proteins (Sibley 1970, Sibley & Ahlquist 1972), blood proteins, lipids in secretions of the uropygial gland (Jacob, see Jacob & Ziswiler 1982), comparisons of total DNA content of the nucleus (Sibley & Ahlquist 1990), and finally sequencing of M-DNA (Shields & Helm-Bychowski 1988, Avise 1986) and of nuclear DNA.

Considerable attention has been given to whether a phenetic, a cladistic or an evolutionary approach provides the best biological classifications. Here, I restrict myself to consideration of a proper methodology for testing taxonomic hypotheses about groups, including the necessary analyses of taxonomic properties of characters. This methodology should be common to all approaches to classification, be they phenetic, cladistic or evolutionary.

During the past 40 years, considerable attention has been given to the analysis of large sets of taxonomic characters using sophisticated computer-based numerical techniques (generally some type of correlation analysis such as PAUP or Hennig86), in the attempt to obtain the best and most "parsimonious" classification. However, what has been almost completely lacking during the past 40 years are considerations of the analysis of the taxonomic characters themselves, both in theory and in actual studies. These methods include how different types of group hypotheses are tested against hypotheses about taxonomic properties of characters, how these character hypotheses are tested themselves against empirical observations, and the role of functional and adaptive analyses in character analysis. Theoretical papers such as Cracraft (1981a), Raikow (1985), Cracraft & Mindell (1989) and practical systematic studies, such as Cracraft (1974), Bledsoe (1988), Cracraft (1981b), Gauthier (1986), Swierczewski & Raikow (1981), Simpson & Cracraft (1981), Sibley & Ahlquist (1990), and McKitrick (1991), offer sweeping conclusions on the relationships and classification of birds, based, indeed, on intensive comparative description of old and new taxonomic characters and on elaborate computer-based analyses of data sets of these characters. But one will search in vain in these papers for any biological understanding of these taxonomic characters. In spite of the sophisticated methods used for describing some of the characters and of the excellent computer-based methodologies, these studies continue to be founded on character analyses predating Darwin's 'On the Origin of Species' and the subsequent acceptance of evolutionary concepts by biologists. Herein lies, in my opinion, the basic failure in avian macrosystematics.

One part of the solution lies in the clarification of the nature of biological classifications—what they are and for what purposes they are used—and the type of scientific explanation involved in establishing them. The other and perhaps the most significant part of the solution lies in the erecting of a methodology for the formulation of hypotheses at several levels and their testing, with careful attention given to the proper empirical observations used in the last step of the testing procedure. This methodology must be in close agreement with detailed aspects of accepted evolutionary theory, not just with a simplistic statement that organisms have evolved. If the evolution of phenotypic features results from selective demands arising from the external environment, i.e. is adaptive or coupled with adaptive evolution of other features, then the methods of macrosystematics must depend on functional-adaptive studies. The critical roles of these studies are in testing taxonomic properties of characters against empirical observations and in the establishment of degrees of confidence in the conclusions of these tests. These are topics on which I have devoted considerable effort and have published a series of papers (Bock 1959, 1965, 1967, 1969, 1973, 1977a, 1977b, 1978, 1979, 1980, 1981, 1988, 1989a, 1989b, 1990, 1991, Bock & de W. Miller 1959, Bock & von Wahlert 1965, Szalay & Bock 1991), to which the interested reader is referred for a full theoretical foundation of the points made in this paper.

It should be stressed that the ideas developed in these papers on hypotheses formation and testing and on the essential role of functional/adaptive studies are valid regardless of the approach to classification. Although these ideas are dependent on a full understanding of evolutionary theory, they are not restricted to evolutionary classification, but are equally valid for cladistic and phenetic approaches to classifications. However, a clear distinction must be made between a cladistic approach to classification and the so-called cladistic method of analysis; I consider the latter to be scientifically invalid (Bock 1981: 15). A distinction should also be made between cladistic and phylogenetic methods. Moreover, the various computer-based methods for formulating classifications on data sets, such as Hennig86 or PAUP, will work equally well with characters analyzed using these methods, because they depend only on an ordered character set and do not depend on how one has determined the information about the characters and their states.

These theoretical concepts will be illustrated by the use of several actual examples, in which more convincing conclusions have been reached using the methods mentioned above when compared with studies in which functional-adaptive investigations were not used.

THE CONCEPT OF BIOLOGICAL CLASSIFICATION

The concept and use of classifications in any science, including biological classification, are generally poorly understood in spite of their widespread use. Simply put, classifications are heuristic systems, no more and no less

(Warburton 1967, Bock 1973), but none the less valuable, and careful attention should therefore be given to their form and testing. As heuristic systems, classifications can be constructed according to any set of ideas or criteria depending on how the classification is used. For classifications to be 'natural' or 'general reference systems', they must be formulated according to the primary theory of the appropriate science. Evolutionary theory is the foundation for biological classifications, and hence they should reflect evolutionary theory as closely as possible. By evolutionary theory, I do not mean simply that living organisms have changed over time, rather I mean all aspects of this theory (e.g. "the five theories of evolution of Darwin"—Mayr 1982: 505, 1991: 36–7) including a detailed understanding of the causes and processes of evolutionary change. As emphasized by Hennig (1966: 8), it is complete nonsense to argue, as did Rosen *et al.* (1979), that a "natural order exists in nature", e.g., that "nature's hierarchy exists" independently of any theory and can be discovered with the use of a theory-free methodology.

As heuristic systems, classifications have a number of important uses (Warburton 1967, Bock 1973). Primarily, biological classifications provide the foundation for comparative studies in biology (see Bock 1989a for a discussion of the principles of comparison in biology). They summarize succinctly known empirical information about diverse organisms, and form the basis of information retrieval systems; but classifications are emphatically not information retrieval systems themselves and one cannot obtain directly from any classification the information used 'to construct', or better said to test, that classification. In addition, classifications serve as the foundation on which efficient and meaningful hypotheses can be generated about biological organisms for further research and testing, e.g. the prediction of unknown characteristics. The best natural classifications are those which permit the best summarization of known information and the best prediction of unknown features in diverse organisms.

It must be emphasized strongly that a classification and a phylogeny of a group, e.g. the class Aves, are not synonymous, but are 2 different and valuable methods to record conclusions reached in systematic analyses. Efforts by some systematists, e.g. cladists, to render these 2 systems of representation redundant to each other simply results in losing useful knowledge about the group; and as I have argued elsewhere (Bock 1977b, 1981), methods for testing classifications and for testing phylogenies differ distinctly from each other. Hence, a well carried out macrosystematic study should include in its conclusions both a clearly presented classification and a phylogenetic diagram.

Classifications and phylogenetic diagrams are related explanatory systems in biology and hence it is necessary to inquire into types of explanations involved in both classifications and phylogenetic diagrams. Many theoretical biologists and philosophers of science have claimed that evolutionary biology, being concerned with the history of organic life, is a strictly historical endeavour. A few philosophers have even claimed that because it is concerned only with the history of life, evolutionary theory is not part of science proper. Some systematists (mainly cladists) have claimed that all explanations in evolutionary biology, including systematics, are strictly nomological (Gaffney 1979, Platnick 1979, Platnick & Gaffney 1977) in a desperate effort to bring their work in line with Popperian concepts. Both positions are extreme and invalid, since evolutionary biology involves both nomological-deductive explanations (N-D E) and historical-narrative explanations (H-N E); I have outlined the distinctions between them in several papers (Bock 1981, 1988, 1991). Explanations associated with biological classifications (relationships between organisms) and with phylogenetic diagrams (branching of phylogenetic lineages) are clearly historical-narrative and as such are covered by the methods for formulation and testing H-N E, which depend on the N-D E within evolutionary biology including the known causes and processes of evolutionary change.

HYPOTHESES FORMULATION AND TESTING

If biological classification should reflect all aspects of evolutionary theory, so must the entire methodology of hypotheses formation and testing, including the predictions generated from various hypotheses and their eventual testing against empirical observations under the tenets of H-N E. First it is necessary to distinguish between group hypotheses and character hypotheses (Bock 1977b, 1981).

Group hypotheses in macrosystematics are of 2 types which differ sharply from one another both in their formulation and testing. The first are classificatory hypotheses about taxa which express the evolutionary relationships of the constituent members within a formal hierarchical system under the conventions accepted for evolutionary classification. This formal classification is a Linnaean hierarchy and the rules for recognizing the taxa are those that maximize simultaneously the postulated degree of evolutionary change and the sequence of phylogenetic branching of these groups. The taxa, once recognized, must be monophyletic in that the members of the taxon are descendants from a single ancestral taxon at the same or lower categorical rank.

The second type of group hypotheses are phylogenetic hypotheses about phyla (singular = phylon; see Bock 1977b: 877, 1981: 13) which express the pattern of phylogenetic branching within a formal phylogenetic diagram under the conventions accepted for these diagrams, namely successive dichotomous forks as advocated by Hennig (1966). Groups in this phylogenetic diagram are phyla which are closed descendent groups. The phyla, once recognized, must be holophyletic (Ashlock 1971), that is a group which includes the ancestral species and all descendent species. Phylogenetic hypotheses about groups can express ancestral-descendent relationships in addition to sister-group relationships. For an analysis of phylogenetic hypotheses about groups and their testing see Bock (1977b, 1981), as I restrict myself herein to classificatory hypotheses about groups.

Sequence of hypotheses formulation and testing

Although most taxonomic investigations are usually pursued with little to no attention given to the actual sequence of hypothesis formulation and testing, a definite order of these activities should be used in a formal analysis of macrosystematic methodology, and this sequence should be followed in written presentations (see Bock 1985a, 1985b, Bock & Morony 1978b, Bock & Bühler 1990, for examples). This sequence is as follows:

a) Formulation and statement of classificatory hypotheses about groups

These statements express hypotheses about the composition and evolutionary relationships of taxa which are monophyletic groups in the broad sense. Classificatory hypotheses should be explicit and stated at the beginning of a paper; they are within the realm of H-N E. Classificatory hypotheses are of the sort: is the genus *Diglossa* as recognized in Peters' Check-list monophyletic?; are the diverse species of flowerpiercers members of 2 distinct and not closely related genera, *Diglossa* and *Diglossopis*, within the Thraupinae (Bock 1985a)?; do the palaeognathous birds constitute a monophyletic group?; do the ratites constitute a monophyletic group (Bock & Bühler 1990)?; is the genus *Promerops* a member of the Meliphagidae (Bock 1985b)? Such hypotheses can be answered in the affirmative or negative.

Group hypotheses are easy to formulate, but this is not the important element in macrosystematics. The skill required is to be able to distinguish between those hypotheses worthy of further consideration for serious testing and those which can be disregarded for the present time. There are no reasons to consider seriously at this time, for instance, the testable hypothesis that the genus *Struthio* is a member of the family Corvidae. Moreover, one does not just formulate well-tested hypotheses, an expression used by some avian systematists. Rather, one should propose hypotheses worthy of consideration and then test them sufficiently so that they can be regarded as well-corroborated and usable as foundations for standard classifications and sequences. There are, of course, perfectly good classificatory hypotheses about groups which may not be worthy of consideration and testing at the current time because of an insufficient knowledge about the taxonomic features needed to test them. Formulating any classificatory hypotheses about particular groups and undertaking a comparative investigation of some feature do not of themselves provide a convincing basis for reaching sound conclusions about the classification of these taxa. Not all features are useful taxonomic characters.

b) Formulation and statement of character hypotheses about taxonomic properties of features

Secondary hypotheses about taxonomic properties of features are used to test the classificatory hypotheses about groups, and must be suited to the group hypotheses being considered—the secondary (=character) hypotheses must constitute valid tests regardless of the 'goodness' of the test. Valid tests of group hypotheses are those which relate predictions arising from the group hypotheses through the secondary character hypotheses to empirical observations according to the detailed stipulations of evolutionary theory. 'Good' tests are valid ones with a high ability to distinguish between correct and incorrect hypotheses—that is, possess a high resolving power to separate correct and incorrect answers. Taxonomic properties of features are those relative attributes of features, such as homology, plesiomorphy *versus* apomorphy, arising from the evolutionary history of the group. Hypotheses about taxonomic properties of features are H-N E. At some point within the test of such hypotheses must be appropriate N-D E, namely, the fundamental nomological aspects of evolutionary theory (see Bock 1981, 1988, 1991).

The only valid character hypothesis known to me for the testing of classificatory hypotheses about groups is homology (Bock 1977b, 1981, 1989b). Homologous features (or conditions of the features) in 2 or more organisms are those that stem phylogenetically from the same feature (or condition) in the immediate common ancestor of these organisms (Bock 1989b: 331). Hypotheses about homologues must always include a conditional phrase that describes the nature of the homology—i.e. the attributes of the feature in the immediate common ancestor. Conditional phrases are arranged into hierarchies – horizontal ones for the purposes of this analysis dealing with classificatory hypotheses.

Several widely used tests of classificatory hypotheses are, however, invalid (Bock 1981) and include those using criteria such as parsimony, or internal consistency or logic, or parallelism with changes in ontogeny, or distribution of character states in taxonomic groups. The last includes the almost universally used method of out-group comparison in cladistic analysis. This method is directly circular (Bock 1981: 15) because the test of the character hypotheses depends on the distribution of the character states in taxonomic groups and these character hypotheses are then used to test classificatory hypotheses about the same taxonomic groups.

The only valid test of hypotheses about homologues involves all forms of shared similarities between the presumed homologues; observations of these similarities comprise the objective empirical observations required in testing scientific hypotheses (Bock 1981, 1989b). Similarity of presumed homologous features is assumed to represent 'ancestral similarity', namely, the attributes present in the feature in the immediate common ancestor of the several organisms being compared, and which remained unchanged during evolution of the different lineages from the common ancestor. It must be emphasized that the defining criterion of homology is phylogeny and that phylogeny is defined in terms of evolution. Similarity is used to test hypotheses about homologous features, not to define the concept of homology. The difference between phylogeny and similarity is the distinction between the criterion used in *defining* theoretical concepts and that used in *testing* hypotheses about objects in nature presumably corresponding to the theoretical concepts. Only after being tested positively using empirical observations of similarity, are homologous features in diverse organisms then used to test classificatory hypotheses about taxa containing these organisms. No circular reasoning is involved in this analysis as frequently argued. Homologous features are not ascertained and tested by the phylogeny of groups and then used to test the phylogeny of these groups.

c) Establishing degrees of confidence

After testing and accepting hypotheses about the homology of features with properly stated conditional phrases, the next step is to estimate a degree of confidence ('goodness') for each homology, since the only valid test of hypotheses about homology distinguishes between correct and incorrect ones very poorly. If the hypothesis about the homology *has been accepted*, then the determination of a degree of confidence does not increase its acceptance. As is well known similarity of features in diverse organisms can be homoplastic as the result of independent origin and convergent evolution. Estimation of a degree of confidence in a particular homology is a probability measure, considering concepts of Bayesian probability, and depends largely on approximation of the probability that the features involved originated and underwent similar evolutionary change independently. These estimates must be based on the accepted principles of evolutionary change and on the evolutionary changes possible in the class of features containing the homologues, that is, how bones evolve, how muscles evolve, etc. Essentially, they depend on functional and adaptational analyses of the features, with the postulation of possible transformation sequences (that is, phylogenetic reconstruction series) based on these analyses.

Estimating the degree of confidence in accepted hypotheses about taxonomic properties of features is that aspect of systematics usually termed 'weighing of characters' or 'ascertaining the taxonomic value of characters'. Most discussions of character weighing, although inherently reasonable, have never been placed on a sound theoretical basis. Moreover, evaluation of degrees of confidence must be done *a priori*, not *a posteriori*, to the use of these character hypotheses in testing group hypotheses.

The degree of confidence will depend strongly on the complexity of the actual feature, its relationship with factors of the external environments and hence with selective demands, and whether the feature is appearing or being lost in evolution, etc. If the homologous feature is a simple one, such as the brown colour of the plumage in different species of sparrows which serves as protective colouration, then one may well assign it a very low degree of confidence. If the feature is a complex one, such as the Weberian sound-transmitting ossicles derived from vertebral processes in a number of fresh-water teleost fishes, one is justified in estimating a high degree of confidence. Generally, the degree of confidence is higher in homologues which have appeared and are becoming more complex during their evolution than in those which are disappearing or becoming simpler. Many of the considerations given by taxonomists about criteria for homology (e.g. Rieger & Tyler 1979) or to an estimate of the taxonomic values of different characters (Hecht & Edwards 1977) are actually methods establishing confidence in accepted conclusions about homologies.

Estimation of these degrees of confidence is an absolute requirement in macrosystematic analysis because so many apparent homologues have an exceedingly low probability of being correct. It is simply not valid to use equally all successfully tested homologies in the testing of group hypotheses. Homologies with low degrees of confidence have little or no value in tests of group hypotheses, contrary to the beliefs of many systematists. Unfortunately no studies have been done using the concepts of decision theory on the contribution of homologues with varying degrees of confidence in accepted group hypotheses. However, some rough estimates suggest that even several hundred independent homologues, each having a degree of confidence of less than 10% will provide a poor test of a group hypothesis. A much smaller number of independent homologues, perhaps 10 or even fewer, each having a degree of confidence of over 90% may provide a very convincing positive test of a group hypothesis. The long lists of untested postulated homologues given in numerous taxonomic papers may appear convincing at first glance, but they become far less impressive when one realizes that no attempt has been made to state the hypotheses of homologies clearly, let alone to establish degrees of confidence in the homologues involved. Generally little work is required to demonstrate that most of the homologous features in the long lists possess low levels of confidence.

d) Testing of group hypotheses

Each classificatory hypothesis about groups is tested against a number of separate character hypotheses about homology, each of which has been tested against empirical observations completely independently of the others. As already indicated, increase in the degree of confidence in group hypotheses is gained with increase in the number of tests against different homologous features possessing a high degree of confidence.

Each empirical test of a character hypothesis about homologies must be absolutely independent of all others. Otherwise the different homologues will not provide independent tests—they are redundant—as stressed by Bock (1977, 1981, 1989b). Examination of the criteria for homology advocated by some authors (e.g. Remane 1952), demonstrates that some are either not independent of other homologues or are not independent of the group hypothesis being tested. Homologues tested with such criteria would not provide additional independent valid tests of the group hypothesis and hence would not increase the confidence in the correctness of the group hypothesis. Continued testing of a group hypothesis against more and more character hypotheses possessing low degrees of confidence simply does not add to the confidence already attained.

The single major defect in many papers on macrosystematics lies in the use of character hypotheses possessing low degrees of confidence for testing group hypotheses. Close examination of the large number of taxonomic characters cited by Gauthier (1986) supporting his conclusion that birds are most closely related to the Coelurosauria of the theropod dinosaurs finds only low degrees of confidence in the homologues; therefore his group hypothesis has a corresponding low degree of confidence. McKitrick (1991) has recently published a most interesting phylogenetic analysis of birds using their hindlimb musculature; she presents a phylogeny and compares her conclusions with various recent classifications, but she does not present any classificatory hypotheses herself. Close study of McKitrick's paper suggests that a serious shortcoming lies in the low degree of confidence in the homologies of the several character states described for each hindlimb muscle; hence any classificatory hypothesis about avian taxa tested against these homologues would have a correspondingly low degree of confidence.

The recently published classification of birds by Sibley & Ahlquist (1990), advocating major modifications in the relationships of avian orders and families, depends entirely on the degree of confidence that can be established for the homology of avian DNA, in as far as Sibley & Ahlquist have described and compared it in the diverse taxa of birds. It must be emphasized that they have never described the homologies of the fragments of DNA subjected to the annealing comparisons used in their analysis and have therefore presumably never tested the homology of these DNA fragments directly; nor have they provided any estimate of the degree of confidence for each conclusion about the fragments of DNA. They have merely presumed them to be homologous and have assumed a high degree of confidence in *all* homologies regardless of the extent of annealing of DNA from different taxa, even at the lowest percent of annealing. Contrary to the claims of Sibley & Ahlquist and some other workers, they have not solved the 'problem of homology'. If one concludes, as I do, that the degree of confidence is low for each (unstated) individual test of homology of the many different fragments of DNA in the comparisons made by Sibley & Ahlquist, then the degree of confidence in their classificatory hypotheses would be correspondingly low. The fact that the annealing comparisons involve a large number of fragments of the DNA of the taxa compared does not raise the degree of confidence, as they claim, in the test of the group hypotheses. The degree of confidence in a group hypothesis is *not* ascertained by a simple addition of the degrees of confidence of the individual character hypotheses used to test the group hypothesis. Rather the degree of confidence in the group hypothesis is largely determined by the degree of confidence in the individual character hypotheses.

e) The method of reciprocal illumination

A major point made by Hennig (1966: 21) is that "In reality, phylogenetic systematics uses a method known and employed in all sciences, which in the humanities is called the 'method of reciprocal illumination' (checking, correcting and rechecking of the Anglo-Saxon authors)." Hennig suggests that this method involves the formulation of a series of character hypotheses, and from this series a group hypothesis is generated, which in turn is then used to check further the validity of the original character hypotheses which in turn are again used to check further the group hypothesis (Hennig 1966: 22). If I understand this statement correctly, it is circular in spite of the strenuous protesting of Hennig against this conclusion. This method has been cited with approval by cladistic systematists and a number of philosophers of biology, but without real clarification of the exact procedure employed. Either the method of reciprocal illumination as outlined by Hennig is circular or the description of the proper working procedure is obscure. "Checking, correcting and rechecking" can be interpreted completely differently, as an approach which involves the testing of a group hypothesis using a series of independently tested character hypothesis, thereafter reformulating the group hypothesis depending on the outcome of these independent tests, followed by further testing of the modified group hypothesis using a series of independently tested character hypotheses, including new ones not used in the test of the original group hypothesis. Bühler (1980) outlined this approach within the realm of

N-D E in functional morphology. This is a completely different approach from that described by Hennig as I understand it. If this is the approach to be used, then the better name would be 'the method of multiple independent tests' rather than 'the method of reciprocal illumination'.

CASE STUDIES

If the above argument on the central role of functional-adaptive analyses in macrosystematics is acceptable, then it should be possible to demonstrate with case studies that the use of this approach has permitted a better understanding of difficult problems in macrosystematics.

Relationship within the plovers (Charadriidae)

In a series of papers, P. R. Lowe (see 1922; see also Bock 1958 for citations to other papers) discussed the relationship of charadriid genera based largely on the ossification of the supraorbital rims of the brain case and the colour of the back. He argued that the primitive genera possessed less ossified supraorbital rims and a light dorsal colour and that the advanced genera had more ossified supraorbital rims and a dark dorsal colouration. Although reviews critical of Lowe's papers were published, many of his general conclusions formed the basis of the classification of this family in Peters' Check-list. Nowhere in his papers did Lowe attempt any functional-adaptive analyses; he judged that the less ossified supraorbital rims and lighter colour were primitive ("adumbrated"), claiming these were the initial attempt by nature to produce these features, and that the more ossified rims and darker colour are the more complete (finished) product. In addition, he claimed that the primitive, less ossified supraorbital rims represented the earlier stage in the ontogenetic development of these rims, through which the more ossified rims passed earlier in their ontogeny. He argued strongly that these features are not directly affected by the present-day environment, but represent conditions inherited unchanged from the ancestral state.

In analysing these features in my generic review of the plovers (Bock 1958), I found the colouration of the dorsum easy to explain. Ever since Professor Alfred Newton suggested to H. B. Tristram in 1858 (letter dated 24 August 1858—Wollaston 1921: 111–117) that Tristram should read the then recently published papers by Darwin and Wallace to explain the observed diversity of dorsal colour in African larks, there have been numerous papers showing that the dorsal colouration in open country birds such as plovers, larks, etc. matches the colour of the substrate closely as protective colouration. For Lowe to claim otherwise would require extensive supporting evidence which he did not provide. Alteration in dorsal colour would occur rapidly in the evolution of different species of plovers accompanying changes in the colour of the substrate. Moreover, this evolutionary change would readily occur independently and would revert equally readily with reverse modification of the substrate colour.

The degree of ossification of the supraorbital rims is almost equally easy to explain in terms of functional and adaptive significances. Ossification of these rims is inversely correlated with the size of the nasal glands lying in a supraorbital position; larger glands press more on the bone, cause its de-ossification and hence reduction in the size of the rims. These glands secrete salt and their size is directly correlated with the salinity of the environment of diverse species. Evolutionary changes in size of the supraorbital rims would track changes in the salinity of the environment, would occur independently in diverse species and would reverse with increase and decrease in environmental salinity. Indeed great changes in the size of the supraorbital rims can be observed in a single individual during its life correlated with changes in the salinity of its environment.

Hence it can be shown by rather simple functional-adaptive analyses that the different observed states in these 2 characters are either not homologous or, if concluded to be homologous in diverse species of plovers, they possess a very low degree of confidence, with no possibility of establishing which are the primitive and which are the advanced characteristics in present-day plovers. Their observed states possess a high degree of homoplasy because of their high probability of independent evolutionary origin and reverse evolution. Classificatory hypotheses about taxa within the plovers accepted after testing against Lowe's characters would have exceedingly low degrees of confidence because of the corresponding low degrees of confidence in the character hypotheses. In simple words, dorsal colouration and supraorbital rims in the plovers are poor taxonomic characters.

The palaeognathous birds

The palaeognathous birds comprise the larger flightless ratites and the smaller flying tinamous. The question of whether the palaeognathous birds or the ratites or both constitute monophyletic taxa has been argued by ornithologists ever since these birds were known. Originally the flightless ratites were considered to be a monophyletic group, but not closely related to the flying tinamous. T. H. Huxley (1867) placed the large flightless ratites in the Ratitae, and the tinamous in the Carinatae, together with the other carinate birds. Subsequently some workers (e.g. Wetmore 1940) placed the tinamous together with the ratites in a separate superorder, the Palaeognathae, a monophyletic group within the Neornithes. Gradually during this century most ornithologists have come to agree that the palaeognathous birds and the ratites are polyphyletic groups. Most avian classifications published after 1940 did not recognize the superorder Palaeognathae largely as a result of McDowell's conclusions (1948) that the palaeognathous palate is not homologous in these birds, but also because of the disjunct distribution of the flightless birds. The several families of ratites and tinamous were separated into a number of distinct orders which were placed next to one another in standard sequences simply because ornithologists had no clues to their relationships to other birds. However, a few workers (e.g. Glutz von Blotzheim 1958) still argued for the monophyly of the ratites leaving the question of the classification of the palaeognathous birds unresolved.

A resolution of this question was achieved a few years later when Bock (1963) showed that a complex suite of cranial characters are all homologous in the palaeognathous birds, namely the palaeognathous palate, the posterior position of the basipterygoid process and articulation with the pterygoid, the large zygomatic process lying along the lateral side of the quadrate and closely applied to it, the gap between the maxilla and the maxillary process of the nasal, and the continuity of the ossified orbital and nasal septa (resulting in rhynchokinesis). Moreover, the degree of confidence in these homologues was estimated to be high. All these features had been known previously, but a functional-adaptive investigation permitted the estimation of a high degree of confidence in the character hypotheses and hence in the classificatory hypothesis that the ratites and tinamous constituted a monophyletic taxon. No other classificatory hypotheses were proposed and tested. This classificatory hypothesis was supported by other workers, including Meise (1963), though he considered only the ratites.

The question of the interrelationships of the palaeognathous birds remained, with considerable diversity of opinions on the placement of some taxa within the entire group (Sibley & Ahlquist 1972, 1981, 1990, Cracraft 1974, 1981b, 1988, Bledsoe 1988). However, some conclusions were widely accepted. The tinamous were considered to be a separate taxon and a sister group of the monophyletic ratites. The ostriches and rheas were regarded as sister groups, forming a monophyletic taxon within the ratites.

In a subsequent study, Bock & Bühler (1990) tested a series of classificatory hypotheses, including: whether the Ratitae are a monophyletic taxon? (no); whether the Struthionidae and the Rheidae are sister groups? (no); whether the Struthionidae and perhaps the Aepyronithidae are a monophyletic taxon within the palaeognathous birds? (yes); and, whether the Tinamidae, Rheidae, Casuariidae, Dromaiidae, Apterygidae and Dinornithidae constitute a monophyletic taxon within the palaeognathous birds? (yes). These hypotheses were tested against character hypotheses about the homology of the complex tongue apparatus in these birds. A number of skeletomuscular attributes of the tongue apparatus present in the ostriches are not homologous with those present in the other palaeognathous birds. Moreover, it could be argued that the 2 different configurations of the tongue apparatus present in the palaeognathous birds could not have evolved from each other, but rather each type of reduced tongue evolved independently from a well-developed tongue in the immediate common ancestor of the 2 monophyletic taxa within the palaeognathous birds. The character hypotheses possess high degrees of confidence, and hence the group hypotheses tested against them also possess high degrees of confidence.

Bock & Bühler's classificatory hypotheses differed in several important aspects from previous conclusions. They concluded that the Ratites are not monophyletic within a monophyletic Palaeognathae, and that the Tinamidae is not the sister group of all ratites, but of the Rheidae. These conclusions are radically different from those presented by Sibley & Ahlquist (1981, 1990) based on DNA studies. Assessment of which of these disparate conclusions, if either, are correct depends largely on an evaluation of the degrees of confidence in exact character homologues, particularly of those DNA fragments used by Sibley & Ahlquist to test their several conclusions about palaeognathous birds.

Neotropical flowerpiercers

A small group of 10–17 species of Neotropical nectar-feeding birds found in the mountainous forests from Mexico to Argentina, commonly called flowerpiercers because of their method of cutting into the corolla of flowers to obtain nectar, had been placed in a monotypic genus *Diglossa* ever since their discovery until Bock's (1985a) classificatory hypotheses that the flowerpiercers are members of 2 genera, *Diglossa* and *Diglossopis*, and that these genera are not closely related to one another within the New World 9 primaried oscines, e.g., the Thraupinae. The hypotheses were tested against a series of character hypotheses about the homology of features in the skull, the corneous tongue and the rhamphotheca of these species. The conclusions that these features are not homologous in the 2 groups of species permitted acceptance of the classificatory hypotheses. A brief functional-adaptive analysis of the corneous tongue, which serves to obtain nectar, was critical to this decision and the accompanying conclusion that the 2 genera evolved flower-piercing habits and associated specializations independently.

The passerine finches

The classification of Old World finches has been a major problem for systematists from the beginnings of avian classification. During this century the passerine finches (*Passer* and its relatives) have usually been placed in the Ploceidae, sometimes in a separate subfamily as in Peters' Check-list. The discovery (Bock & Morony 1978a) of a unique neomorphic bone, the preglossale, in the tongue of these birds permitted the testing of the classificatory hypotheses that the genera *Passer, Montifringilla* and *Petronia* constitute a monophyletic assemblage and that this group is not part of the Ploceidae (Bock & Morony 1978b). These group hypotheses were supported by the homology of the preglossale, the presence (homology) of the M. hypoglossus anterior, and the homology of the 'seed-cup' in these genera. Functional analyses of the thick corneous tongue in seed-eating passerine birds as a seed-cup used to manipulate seeds during their shelling and an understanding of the evolution of muscles and bones in vertebrates gave the character and corresponding group hypotheses high degrees of confidence. This was contrary to the conclusions of Sibley & Ahlquist (1985: 144), which, however, they later (1990: 675–683) changed to agree with Bock & Morony without comment on their earlier conclusions. Although the affinities of the passerine finches to other oscine birds is still unresolved, their membership in the Ploceidae and the Estrildidae can be ruled out.

The South African sugar bird

The curious genus *Promerops*, or Sugar Bird, from South Africa has defied avian systematists in their attempts to place it within the system of oscine birds. It has usually been placed in a monotypic family or in the Australasian family Meliphagidae; the latter placement is puzzling because of the great ocean gap between South Africa and the range of the rest of the Meliphagidae. Sibley & Ahlquist (1985: 144, 1990: 670–675) concluded on the basis of DNA annealing that *Promerops* is a member of the Nectariniidae. Bock (1985b) tested the dual hypotheses that *Promerops* is a member of the Nectariniidae and that *Promerops* is a member of the Meliphagidae against character hypotheses on homologies of the skull and tongue apparatus. These tests do not support the hypothesis that *Promerops* is a member of the Nectariniidae. Especially important is the non-homology of the thick-walled, quadrifid, fringed, tubular tongue in *Promerops* and the thin-walled double-tubed corneous tongue with few broad, flag-like laciniae in the nectariniids. If *Promerops* is a nectariniid, then the common ancestor of *Promerops* and other nectariniids was not specialized to feed on nectar. Homologies in skull structure and corneous tongue of *Promerops* and of the meliphagids support the hypothesis that *Promerops* is a member of the Meliphagidae, but they do not possess high degrees of confidence. Although it is not possible at present to distinguish *Promerops* from the Meliphagidae, it is still possible that the South African Sugar Bird evolved from some other oscine family; but strong arguments can be raised against placement of *Promerops* in the Nectariniidae. It should be noted that Sibley & Ahlquist's argument that *Promerops* is closely related to the New Guinean genera *Toxorhamphus* and *Oedistoma*, and that these 2 latter genera are nectariniids must be examined carefully because these 2 genera share many homologous features of the tongue apparatus with those of the meliphagids and few, if any, with those of the nectariniids.

The piciformes

The monophyly of the Piciformes has been the subject of considerable dispute for the past decade, involving the question whether the families Galbulidae and Bucconidae (jacamars and puffbirds), which are often placed in a distinct suborder—the Galbulae, are members of the Piciformes. All major classifications of birds include the Galbulae in the Piciformes in spite of the thorough analysis of G. Steinbacher (1935), who showed that details of the distal tarsometatarsal condyles and other features associated with the reversed fourth toe in the zygodactyl foot of the Galbulae are strikingly different from those present in the Pici. Unfortunately, he never discussed the significance of his findings for the macrosystematics of the piciform birds. Although Steinbacher (1935: 277) spoke of 4 different '*bauplans*' of zygodactyl feet in birds, this expression is uninformative about their evolution. J. Steinbacher (1937) undertook further investigations of the Galbulae and concluded that they were properly placed in the Piciformes; he did not discuss the findings of G. Steinbacher. It is interesting that Stresemann (1959), who recognized many of Wetmore's suborders as distinct orders, retained the Galbulae in the Piciformes. In companion papers, Swierczewski & Raikow (1981) and Simpson & Cracraft (1981) analyzed the classification of the Piciformes and concluded that this order was monophyletic. Olson (1983) disagreed and concluded that it was polyphyletic and that the Galbulidae and Bucconidae are related to the Coracii (Coraciidae and their allies). Raikow & Cracraft (1983) countered Olson's conclusion. I would like to concentrate on the first part of Olson's conclusion, namely the polyphyletic nature of the Piciformes.

Olson is quite correct in calling attention to the different configurations of the zygodactyl foot in the Galbulae and Pici. Character hypotheses can be formulated as to whether the structural details of the distal tarsometatarsal condyles and associated ligaments of the zygodactyl foot of the Galbulae are homologous with those of the Pici as attributes of a zygodactyl foot. Testing these hypotheses against empirical observations of foot structure in these 2 forms of birds, results in rejection of the hypotheses. [It should be noted that contrary to the implication given by Olson (1983: 127), the earlier analysis of Bock & Miller (1959) was not concerned with the question of whether or not the several different types of zygodactyl feet as seen in cuckoos, parrots, galbulids and picids evolved independently; hence the earlier findings of G. Steinbacher were irrelevant to their analysis.] The functional-adaptive analysis presented by G. Steinbacher (1935) and later discussions of Bock & Miller (1959) can be used to argue that the non-homology of the zygodactyl foot in galbulids and picids has a high degree of confidence. The counter arguments presented by Raikow & Cracraft (1983) simply do not touch on the major points raised by Olson. Moreover, Raikow & Cracraft (1983: 134) commit a major error in stating that "We suggest that the zygodactyl conditions of the Galbulae and Pici are homologous because other characters (see below) corroborate the unity of the Piciformes." Testing and acceptance of a hypothesis on the homology of one feature cannot be based on a presumed affinity of the organisms possessing this feature or on a correlation with other presumed homologous features. By making this statement, Raikow & Cracraft remove the zygodactyl foot from any further use in testing group hypotheses about the Piciformes—a procedure which should be avoided in macrosystematics.

The South American hoatzin

Perhaps of all problems facing avian macrosystematics, the affinities of the hoatzin, *Opisthocomus*, is the most vexing. It was originally described in the genus *Phasianus* in 1776 and only placed in the monotypic genus *Opisthocomus* in 1811. Over the years this bird has generally been placed in the Galliformes or the Cuculiformes, or in a group (a separate order) intermediate between the two, but for the past century most workers have included the hoatzin in the Galliformes as a separate suborder. More recently Sibley & Ahlquist (1973, 1990) have concluded that *Opisthocomus* is a member of the Cuculiformes and is most closely allied to genera such as *Guira* and *Crotophaga*, originally on the basis of a comparison of egg-white proteins and later of DNA annealing. In their extensive discussion of the history of systematic analyses and characteristics of *Opisthocomus*, Sibley & Ahlquist fail to mention an important attribute of this bird (Bock, in press)—namely that the arrangement of the toes in the hoatzin is anisodactyl, not zygodactyl as in all members of the Cuculiformes. Examination of skeletons of *Opisthocomus* shows that this bird lacks completely the specializations described by G. Steinbacher (1935) for the cuckoo tarsometatarsus which are associated with their zygodactyl foot, permitting reversal of tendons to the fourth toe. The zygodactyl foot of cuckoos is an adaptation for perching and is so used in most forms of cuckoos, including those genera concluded by Sibley & Ahlquist to be the closest relatives of the hoatzin. Hoatzins are specialized for life in trees, and if they descended from cuckoos, there is no way that the hoatzin anisodactyl toe arrangement would have evolved from the cuckoo zygodactyl arrangement under selective demands for these habits (Bock & Miller 1959). Hence there is no way to support the conclusion that the hoatzin evolved from an ancestor with a zygodactyl foot such as possessed by cuckoos. Sibley & Ahlquist did not conclude that *Opisthocomus* was a sister group of the cuckoos, but that it evolved from an ancestor in the middle of the cuckoo radiation and therefore from an ancestor possessing a zygodactyl foot. Therefore testing the classificatory hypothesis that *Opisthocomus* is a member of the Cuculiformes against character hypotheses about the homology of toe arrangement would result in its rejection with a high degree of confidence because the arrangements of the toes in the Cuculiformes and in *Opisthocomus* are not homologous with any degree of confidence. At the present time, the position of *Opisthocomus* in the system of birds is uncertain, but it is not a cuckoo. Possibly it is a remnant of an old South American radiation most of which has become extinct; if so, the relationships of the hoatzin to other birds could be difficult to ascertain.

CONCLUSION

The theoretical discussion and the several case studies presented above demonstrate that a convincing classification of birds is almost completely dependent on thorough and proper analyses of character hypotheses, including the demonstration of high degrees of confidence in the taxonomic properties of characters used to test classificatory hypotheses about groups. Functional-adaptive investigations are the critical part of character analysis, both in the empirical testing of the character hypotheses and in the determination of their degrees of confidence. Therefore until avian systematists give careful attention to functional-adaptive investigations in the analysis of the taxonomic properties of characters, no convincing progress will be made in avian macrosystematics regardless of the efforts made in the search for new taxonomic features or in the development of computer methods for analyzing large numbers of characters to formulate the most 'parsimonious' classifications. After nearly 150 years since publication of '*On the Origin of Species*', the time has come to insist that macrosystematic methodology be formulated on evolutionary theory.

Acknowledgements

I would like to thank Dr. J. F. Monk for inviting me to contribute a paper to the Bulletin of the B.O.C. Centenary Supplement and for his excellent assistance in editing the paper, which is much improved through his efforts.

References:

Avise, J. C. 1986. Mitochondrial DNA and the evolutionary genetics of higher animals. *Phil. Trans. Roy. Soc. London*, B 312: 325–342.

Ashlock, P. 1971. Monophyly and associated terms. *Syst. Zool.* 20: 63–69.

Bledsoe, A. H. 1988. A phylogenetic analysis of postcranial skeletal characters of the ratite birds. *Ann. Carnegie Mus.* 57: 73–90.

Bock, W. J. 1958. A generic review of the plovers (Charadriinae, Aves). *Bull. Mus. Comp. Zool.* 118: 27–97.

— 1959. Preadaptation and multiple evolutionary pathways. *Evolution* 13: 194–211.

— 1963. The cranial evidence for ratite affinities. *Proc. XIII Internat. Ornith. Cong.* 1: 39–54.

Bock, W. J. 1965. The role of adaptive mechanisms in the origin of higher levels of organization. *Syst. Zool.* 14: 272–287.

— 1967. The use of adaptive characters in avian classification. *Proc. XIV Internat. Ornith. Cong.* Pp. 61–74.

— 1969. Comparative morphology in systematics. Pp. 411-448. *In:* C. G. Sibley, ed., *Systematic Biology*. Nat. Acad. Sciences.

— 1973. Philosophical foundations of classical evolutionary classification. *Syst. Zool.* 22: 375–392.

— 1977a. Adaptation and the comparative method. *In:* M. Hecht *et al.*, eds. *Major Patterns in Vertebrate Evolution.* NATO Advanced Study Institute. Ser. A, 14: 57–82. Plenum, New York.

— 1977b. Foundations and methods of evolutionary classification. *In:* M. Hecht *et al.*, eds. *Major Patterns in Vertebrate Evolution.* NATO Advanced Study Institute. Ser. A, 14: 851–895. Plenum, New York.

— 1978. Comments on classification as historical narratives. *Syst. Zool.* 27: 362–364.

— 1979. The synthetic explanation of macroevolutionary change—a reductionist approach. *Bull. Carnegie Mus.* 13: 20–69.

— 1980. The definition and recognition of biological adaptation. *Amer. Zool.* 20: 217–227.

— 1981. Functional-adaptive analysis in evolutionary classification. *Amer. Zool.* 21: 5–20.

— 1985a. Is *Diglossa* (? Thraupinae) monophyletic? *Eisenmann Memorial Volume, Ornithological Monographs* (A.O.U.) 36: 319–332.

— 1985b. Relationships of the Sugarbird (*Promerops*; Passeriformes, Meliphagidae). Pp. 349–374. *In: Proc. Internat. Symp. Afr. Vertebrates.* Koenig Museum, Bonn.

— 1988. The nature of explanations in morphology. *Amer. Zool.* 28: 205–215.

— 1989a. Principles of biological comparisons. *Acta Morphol. Neerl.-Scand.* 26: 17–32.

— 1989b. The homology concept: Its philosophical foundation and practical methodology. *Zoolog. Beitr.*, N.F. 32: 327–353.

— 1990. From Biologische Anatomie to Ecomorphology. *Proc. 3rd Internat. Congr. Vertebrate Morphology. Netherl. Jour. Zool.* 40: 254–277.

— 1991. Explanations in Konstruktionsmorphologie and evolutionary morphology. Pp. 9–29. *In:* N. Schmidt-Kitter & K. Vogel, ed. *Constructional Morphology and Evolution.* Springer-Verlag, Heidelberg.

— In Press. Is the hoatzin (*Opisthocomus hoazin*) a cuckoo (Cuculiformes)?

Bock, W. J. & Bühler, P. 1990. The evolutionary and biogeographical history of the palaeognathous birds. Pp. 31–36. *In:* R. van den Elzen, K.-L. Schuchmann & K. Schmidt-Koenig, eds., *Current Topics in Avian Biology.* Ornithologen Gesellschaft, Bonn, 1988.

Bock, W. J. & Miller, W. de W. 1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. *Amer. Mus. Novit.* 1931, 45 pp.

Bock, W. J. & Morony, J. 1978a. The preglossale in *Passer* (Aves: , Passeriformes)—a skeletal neomorph. *Jour. Morph.* 155: 99–110.

—, — 1978b. Relationships of the passerine finches (Passeriformes: Passeridae). *Bonn. Zool. Beitr.*, 91: 49–61.

Bock, W. J. & von Wahlert, G. 1965. Adaptation and the form-function complex. *Evolution* 19: 269–299.

Cracraft, J. 1974. Phylogeny and evolution of the ratite birds. *Ibis* 116: 494–521.

— 1981a. The use of functional and adaptive criteria in phylogenetic systematics. *Amer. Zool.* 21: 21–36.

— 1981b. Toward a phylogenetic classification of the Recent birds of the world (Class Aves). *Auk* 98: 681–714.

— 1988. The major clades of birds. Pp. 333–355. *In:* M. J. Benton, ed., *The Phylogeny and Classification of the Tetrapods.* Vol. I. Oxford University Press.

Cracraft, J. & Mindell, D. P. 1989. The early history of modern birds: a comparison of molecular and morphological evidence. Pp. 389–404. *In:* B. Fernholm *et. al.*, eds., *The Hierarchy of Life. Molecules and Morphology in Phylogenetic Analysis.* Amsterdam, Excerpta Medica.

Gaffney, E. S. 1979. An introduction to the logic of phylogenetic reconstruction. Pp. 79–111. *In:* N. Eldredge and J. Cracraft, eds., *Phylogenetic Analysis and Paleontology.* New York, Columbia University Press.

Gauthier, J. 1986. Saurischian monophyly and the origin of birds. *Calif. Acad. Sci. Mem.* 8: 1–56.

Glutz von Blotzheim, U. 1958. Zur Morphologie und Ontogenese von Schultergürtel, Sternum und Becken von *Struthio, Rhea,* und *Dromiceius. Rev. Suisse Zool.* 65: 609–772.

Hecht, M. K. & Edwards, J. L. 1977. The methodology of phylogenetic inference above the species level. Pp. 3–51. *In:* M. Hecht *et al.*, eds. *Major Patterns in Vertebrate Evolution.* NATO Advanced Study Institute. New York, Plenum, ix + 908 pp.

Hennig, W. 1966. *Phylogenetic Systematics.* Univ. Illinois Press, 263 pp.

Huxley, T. H. 1867. On the classification of birds; and on the taxonomic value of the modifications of certain of the cranial bones observable in that class. *Proc. Zool. Soc.* 27: 415–472.

Jacob, J. & Ziswiler, V. 1982. The uropygial gland. Pp. 199–324. *In:* D. S. Farner, J. R. King & K. C. Parkes, eds. *Avian Biology*, Volume Vl, New York, Academic Press.

Lowe, P. R. 1922. On the significance of certain characters in some charadriine genera, with a provisional classification of the order Charadriiformes. *Ibis* pp. 320–346.

Mayr, E. 1982. *The Growth of Biological Thought. Diversity, Evolution, and Inheritance.* Harvad University Press.

— 1991. *One Long Argument. Charles Darwin and the Genesis of Modern Evolutionary Thought.* Harvard University Press.

McDowell, S. 1848. The bony palate of birds. Part 1. The Palaeognathae. *Auk* 65: 520–549.

McKitrick, M. C. 1991. Phylogenetic analysis of avian hindlimb musculature. *Misc. Publ. Mus. Zool., Univ. Mich.* No. 179: iv + 85 pp.

Meise, W. 1963. Verhalten der Straussartigen Vögel und Monophylie der Ratiten. *Proc. XIII Internat. Ornith. Cong.* 1: 115–125.

Olson, S. L. 1983. Evidence for a polyphyletic origin of the Piciformes. *Auk* 100: 126–133.

Platnick, N. I. 1979. Philosophy and the transformation of systematics. *Syst. Zool.* 28: 537–546.

Platnick, N. I. & Gaffney, E. S. 1977. Systematics: A Popperian perspective. *Syst. Zool.* 26: 360–365.

Raikow, R. J. 1985. Problems in avian classification. *Current Ornithology* 2: 187–212. New York, Plenum Press.

Raikow, R. J. & Cracraft, J. 1983. Monophyly of the Piciformes: a reply to Olson. *Auk* 100: 134–138.

Remane, A. 1952. Die Grundlagen des natürlichen systems, der vergleichenden Anatomie und der Phylogenetik. Theoretische Morphologie und Systematik. Leipzig, Akademische Verlagsgesellschaft Geest & Portig, vi + 364 pp.

Rieger, R. & Tyler, S. 1979. The homology theorem in ultrastructural research. *Amer. Zool.* 19: 635–644.

Rosen, D. E., Nelson, G. & Patterson, C. 1979. Foreword, to W. Hennig, *Phylogenetic Systematics.* Second printing, University of Illinois Press.

Shields, G. F. & Helm-Bychowski, K. M. 1988. Mitochondrial DNA of birds. *Current Ornithology* 5: 273–295.

Sibley, C. G. 1970. A comparative study of the egg-white proteins of passerine birds. *Bull. Peabody Mus. Nat. Hist.* 32: vi + 131 pp.

Sibley, C. G. & Ahlquist, J. E. 1972. A comparative study of the egg-white proteins of non-passerine birds. *Bull. Peabody Mus. Nat. Hist.* 39: vi + 276 pp.

—, — 1973. The relationships of the Hoatzin (*Opisthocomus*). *Auk* 90: 1–13.

—, — 1981. The phylogeny and relationships of the ratite birds as indicated by DNA-DNA hybridization. Pp. 301–335. *In:* G. G. E. Scudder & J. L. Reveal, eds., *Evolution Today.* Pittsburgh, Carnegie-Mellon Univ.

—, — 1985. The relationships of some groups of African birds, based on comparisons of the genetic material, DNA. Pp. 115–161. *Proceedings of the International Symposium of African Vertebrates.* Koenig Museum, Bonn.

—, — 1990. *Phylogeny and Classification of the Birds of the World.* Yale University Press.

Simpson, S. F. & Cracraft, J. 1981. The phylogenetic relationships of the Piciformes (Class Aves). *Auk* 98: 481–494.

Steinbacher, G. 1935. Funktionell-anatomische Untersuchungen an Vogelfüssen mit Wendezehen und Rückzehen. *Journ. f. Ornith.* 83: 214–282.

Steinbacher, J. 1937. Anatomische Untersuchungen über die systematische Stellung der Galbulidae und Bucconidae. *Arch. Naturgesch.*, N.S. 6: 417–515.

Stresemann, E. 1959. The status of avian systematics and its unsolved problems. *Auk* 76: 269–280.22.

Swierczewski, E. V. & Raikow, R. J. 1981. Hind limb morphology, phylogeny, and classification of the Piciformes. *Auk* 98: 466–480.

Szalay, F. & Bock, W. J. 1991. Evolutionary theory and systematics: relationships between process and patterns. *Zeitschrift Zool. Syst. Evolutforsch.* 29: 1–39.

Warburton, F. E. 1967. The purposes of classifications. *Syst. Zool.* 16: 241–245.

Wetmore, A. 1940. A systematic classification for the birds of the world. *Smithsonian Misc. Coll.* 99(7): 1–11.

Wollaston, A. F. R. 1921. *Life of Alfred Newton.* New York, E. P. Dulton & Co.

Address: Dr Walter J. Bock, Department of Biological Sciences, Columbia University, New York, NY 10027, U.S.A.

© British Ornithologists' Club 1992

Subspeciation, clines and contact zones in the southern Afrotropical avifauna

by P. A. Clancey

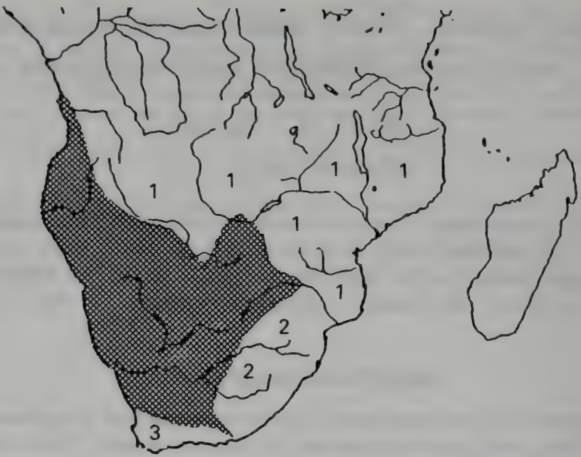
Received 19 February 1991

The following appraisal of current understanding of the complex patterns of variation in resident birds in southern Africa and their interpretation in the recognition of sub- and allospecies, clines and contact zones is presented in order to foster continued research in this vital field of enquiry.

ASPECTS OF SUBSPECIATION

It has been said that subspecies in birds are a matter of opinion, species a matter of fact and genera a matter of convenience. Like all such trite comments, the views expressed are only true in part, but, nevertheless, they correspond with those held by many non-systematists. With effective research, given the requisite material and time to investigate the issues in depth, a conclusion on the desirability of subspecific recognition can assuredly be a statement of fact. The subspecies, albeit sometimes used with a measure of diffidence, will maintain its vital status as the lowest taxonomic category recognised in nomenclatural terms by the International Commission's *Code of Zoological Nomenclature*. It fulfils an integral role in the naming of discrete populations and complexes of distinguishable forms of polytypic species, enabling circumvention of most of the contentious issues encountered by earlier workers who pinned their faith in the maintenance of rigid binomialism. That vertebrates (and others organisms) varied geographically was indeed appreciated by many early taxonomists, who were disposed to rank such variants as full species. Formulation of the subspecies concept dates from about the time of C. W. L. Gloger (1803–1863) and the contemporary publications on evolutionary theory by Charles Darwin.

The effective study of subspeciation in species with largely continuous continental ranges demands ready access to an extensive volume of material, generally far in excess of that held by the largest of museums. In Africa such research is handicapped by the distant siting of basic collections of the continent's birds in European and North American centres, making access difficult and expensive, while in the case of the vital East African sector, virtually all the well-prepared collections formed since the 1939–1945 war are remotely housed in the United States. Conversely, the copious South African and Zimbabwean material brought together since the early 1950s is available in the Southern African Subregion's major museums, and has figured extensively in the research on the avifauna of the south-central, eastern and southern Afrotropics by local ornithologists. In the following discussion I draw freely on data from this research carried out in the south of the continent and to be found in journals of mainly African museums and ornithological societies published between 1950 and 1991.



Map 1. The Afrotropical Region showing the distribution of the South West Arid Zone (shaded) and adjacent environments. 1 = savanna woodlands (mainly Miombo); 2 = mixed forest bushveld and grassland-types; 3 = Cape Fynbos (macchia) and temperate forest.

Variation in the South West Arid Zone

The geographical variation patterns displayed by birds—their races or subspecies—in south-central and southern Africa are in the main prescribed by the disposition of the major plant communities of the South West Arid Zone, which covers rather more than 50% of the Afrotropics south of 16° S. Also influential in this regard are the woodlands of the so-called Miombo savanna juxtaposed to the north and northeast of the said zone, south to the arid valley of the Limpopo R., where the savanna type terminates, these playing a like but rather more restrictive role in the determination of racial range patterns. To the south of these dominant biotic sectors, a mosaic of veld-types, ranging from upland to even alpine grassland, bushveld and, to a limited extent, evergreen forest, both coastal and montane, exert a not indecisive influence in the marked subspeciation of many plastic species.

In a recent study into endemicity levels in birds of regions south of 16° S in Africa, but mainly in the South West Arid Zone, c. 70% of the some 170 regional endemics were found to be peculiar to desertic country, a finding supporting the view that this xeric avifauna had remained largely unaffected by the climatic and biome oscillations of the Pleistocene and immediate subsequent times. In contrast, the eastern and southern veld-types present to the south of the Miombo savanna woodlands (which support an interesting range of endemics) are poorly endowed with species peculiar to them, this being the outcome undoubtedly of the ecological history of such habitats stemming from the disturbing expansions and contractions of the Lower Guinea Forest. Such major disruptions affected savanna bird species in particular, leaving to this day their indelible imprint stratified west to east and in the ripple-like configuration revealed in the range-maps of many species and species-groups. In such situations, the remnant form derived from the primal colonization—now at the level of a discrete species—is confined to a narrow range in the southwestern corner of Africa, with the descendants of later expansionary thrusts lying stratified and at differing stages of evolutionary development disposed to its north and northeast. That the ranges of the individual forms are not infrequently wholly or partially interlarded by untenanted tracts of country is of no small biogeographical significance. This is lucidly demonstrated in the barred bush warblers of the genera *Calamonastes* and *Euryptila* (Clancey 1986, esp. Fig. 3, p. 258).

The broad pattern of savanna species distribution reveals a pronounced continental bias from the northeast to the south in species recruitment, and surprisingly little in the reverse direction. That such southward oriented augmentation is not a thing of the past is clearly illustrated in the increasing occurrence of the Golden Pipit *Timetothylacus tenellus*—an endemic characteristic of the North Eastern Arid Zone—in the northeast of southern Africa from Zimbabwe to the plateau of the Transvaal. Analogous situations exist in some species which extend far beyond the Afrotropics, as instanced by the Long-billed Pipit *Anthus similis*, which extends from the desertic south of the central Palaearctic and northwestern Indomalaya to the northeastern and southwestern drier country of the Afrotropics. These 2 Afrotropical population groups are separated from one another by intrusive elements of the confusingly similar Wood Pipit *Anthus nyassae*, a pipit of the Miombo biome of south-central Africa and discrete from *similis* in both morphology and ecology, which derives from a like but earlier lineage to that of the contemporary *A. similis* (see especially Clancey 1985). The occurrence of *similis* in the southern parts of Africa was seemingly accomplished by leap-frog colonization across unsuitable country and the savanna woodlands inhabited by *nyassae* subspp.

The broad spectrum of the Palaearctic/Afrotropical bird migration system also furnishes instructive similarities, especially so in the cases of northern species which, through the millenia, have founded colonies in Africa, again in the east and south of the continent. Noteworthily, these again are birds of largely open country environments, particularly savanna types, and not of heavy forest. These colonizations tend to underscore the overriding ecological impact which the seasonal unsuitability of the northernmost sector of the Eurasian landmass has for long exerted in the development of survival strategies in many birds; whereas comparable conditions in the southern hemisphere are only to be found to a limited extent in the south of South America and still less so in southern Australasia.

The broad patterns of geographical variation in southern African birds and their taxonomic interpretation are closely correlated with major vegetational facies and precipitation gradients, conforming closely with those found elsewhere in the world where habitats range sequentially from hygric forest, moist and dry savanna to near absolute desert. In species characteristic of the South West Arid ecosystem, mensural variation is circumscribed in inhabitants of savanna woodland-types, but is pronounced in terrestrial feeders such as larks, in which the length and mass of the bill may visibly increase in clear reaction to the hardness of the substrate. For example, there is a marked increase in the bill-mass in 2 karooid races of the Sabota Lark *Mirafra sabota* (*M.s. bradfieldi* and *herero*) compared with its other subspecies, of which there are 8, and which are relatively slender billed by comparison. Substrate-related variation in bill-form also occurs in forms of *Certhilauda* spp., especially in the Long-billed Lark *C. curvirostris* and the isolated Red Lark *C. (erythrochlamys) burra*, which hybridizes on its periphery with the more slender-billed Karoo Lark *C. albescens*. Just to complicate matters, there is a marked difference in bill-length and profile between the sexes in certain of the *Certhilauda* taxa, yet, interestingly enough, such plasticity in bill-facies is not evident in nearly all other sympatric alaudids.

The plumage of larks, perhaps more so than other terrestrial birds, also varies with local shifts in ground-colour as well as texture (as clearly shown by Hoesch & Niethammer 1940), yet their overall variation patterns are concordant in many respects with those of polytypic species not overtly affected by edaphic factors, such as the equally terrestrial pipits (*Anthus* spp.). Response to local changes in soil-colour reaches its extreme in the mosaic of subspecific forms in the Spike-heeled Lark *Chersomanes albofasciata*, which highly variable species is centred on the arid zone, but which extends in to country to the southeast and north of its core, and has even founded a distant isolate population in northern Tanzania. Despite the high measure of purely localized response to soil-colour change, the overall pattern in *C. albofasciata* is in line with the norm, in that the more deeply coloured races are found in the mesic south and southeast and the palest along the xeric edge of the Namib in northwestern Namibia. The change from dark to light is a progressional or clinally stepped mosaic-cum-gradient. Fourteen subspecies of *C. albofasciata* are admitted in the 1980 *S.A.O.S. Checklist* for the Southern African Subregion alone, while yet others have been proposed.

In moderately polytypic species other than larks centred on the arid zone, relevant taxonomic variation is generally accommodated by the formal recognition of 4 or more subspecies on characters analogous to those just outlined for austral African larks. In considering other instances of edaphic and phenotypic reaction, the status of both localized and widely fragmented populations breeding on the glaring substrate of saline pans in the interior of northern Namibia and the Kalahari region of Botswana, northeast to northwestern Zimbabwe requires to be mentioned, since more than just larks are affected. These interior localized saline pans are tenanted, often seasonally, by very pallid forms of francolin (*Francolinus levaillantoides* subspp.), sandplovers *Charadrius* spp., coursers *Cursorius* & *Rhinoptilus* spp., sandgrouse *Pterocles* spp., small nomadic larks of the genera *Calandrella*, *Spizocorys* and *Eremopterix*, and pipits *Anthus* spp. Environmental glare and not soil-colour is seen as the deciding factor in determining the colouration of such salt-pan forms.

Variation in the mesic sectors

In the wide range of moister habitats arcing round the arid sector on 3 sides, conditions for extensive subspeciation among savanna breeders exist, yet, significantly enough, these same habitats carry many fewer endemics. This is an outcome of the dynamics of the biota's Quaternary past. Study of some of the relicts reveals they have responded to the interplay of local ecological factors, for example in both the localized Ground Woodpecker *Geocolaptes olivaceus* and the Knysna Woodpecker *Campethera notata. G. olivaceus* is an aberrant eurytopic picid of both Karoo and Afro-montane grassland types, and at some stage in its evolutionary history its range was split and polarized in western and in eastern refugia, the 2 populations later meeting in a zone of secondary contact in the eastern Cape Province (see Clancey 1988). Recent study has confirmed that 3 races are admissible and that an earlier recommendation that the variation was clinal and the species monotypic was unjustified (*pace* Earlé 1986). Regional variation in the forestal *C. notata* pursues a different course, its disposition and morphology being dictated by the nature of its woodland niche, with one race centred on stands of *Euphorbia* and dry bushveld and the other on coastal evergreen rain-forest and its remnants. Its phylogenetic status is somewhat clearer than that of *G. olivaceus*, as its general colour saturation, green colouration and heavy black ventral spotting connote a relationship with contemporary equatorial forest woodpeckers.

In some complexes of what may be termed residual relicts, i.e. relict species without verifiable extinct or surviving relatives, the ancient splitting of the deep southern Afrotropical avifauna into 2 small refugial areas at one stage furnished the isolating mechanism basic to the development of allospecific pairs in the region, as in the sugarbirds *Promerops cafer* and *P. gurneyi*, the rockjumpers *Chaetops frenatus* and *Ch. aurantius* and in the siskins *Pseudochloroptila totta* and *Ps. symonsi*. These allospecific pairs are narrowly distributed west to east in association with the main mountain ranges from the western Cape to the Drakensberg complex in the east, though in each instance the individual species of the pairs are spatially segregated in the critical eastern Cape region (the putative site of the ancient refugial rift). In the case of *P. gurneyi*, a major range extension must have occurred at some stage to found the population present in the eastern Zimbabwe frontier mountains (*P.g. ardens*), and similarly in the endemic bush shrike *Telophorus zeylonus*.

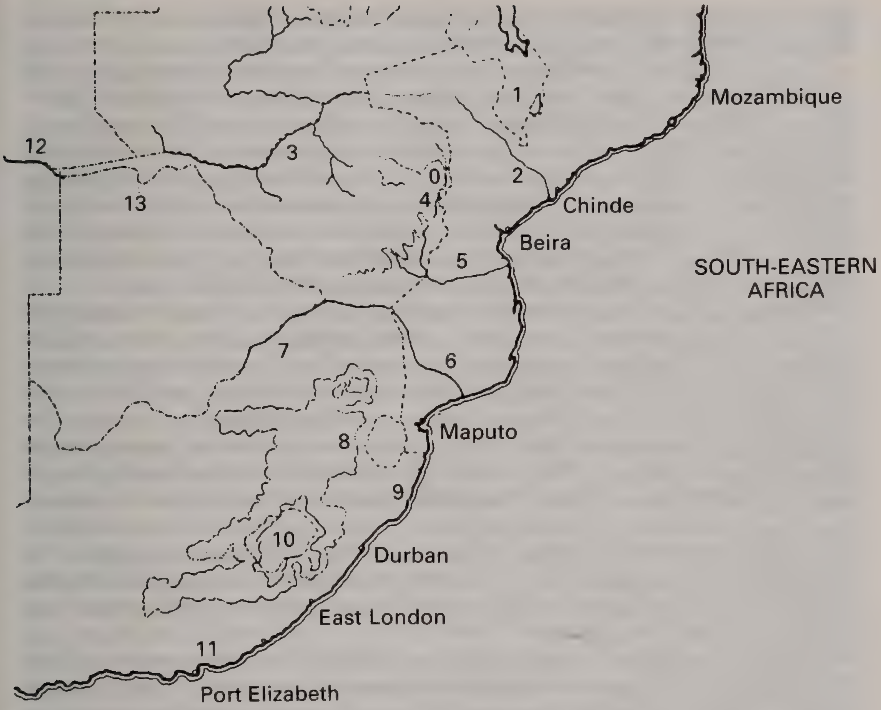
A singularly important faunal area is that of the ecotone which separates the *Julbernardia/Brachystegia* woodland savanna (Miombo) of south-central Africa from the *Acacia* and associated dry-country vegetation to its south, and which is distributed from southern Angola and northern Namibia eastwards. Here the geographical variation in many birds is in the form of a marked increase in overall size together with the assumption of greyer colouration over the upper-parts, and in some there is a decided thickening of the bill, for example in the race of Red-eyed Dove *Streptopelia semitorquata maxima* and that of the Thick-billed Weaver *Amblyospiza albifrons maxima*; the latter, significantly, parallels a comparable increase in bill-mass in the races of the Yellow-rumped Bishop *Euplectes capensis* in the Cape's Winter Rainfall District. The ecological basis of the increase in size and colour modification in such residents of the southern Angola/northern Namibia ecotone is currently obscure.

The avifauna of the mid-Kunene R. to the west of the ecotone has its composition effectively modified by the ambient aridity of the rivercourse as it transects the Namib. On the other hand, the Okavango R. to the east, which flows through the same ecotone, supports an essentially riverine avifauna, which is disparate yet richer in its species composition. This results from the river's flanking vegetation permitting several forms from the hygric parts of central and northern Angola to penetrate the northeast of the South West Arid Zone. Nevertheless, the vegetation of the mid-Kunene also facilitates some southward range extension in species with equatorial but rather more western affinities. For example, the Kunene race of *S. semitorquata* is the nominate, with *S.s. maxima* (see above) replacing it along the Okavango (Clancey 1986a, 1989b); in the Green Pigeon *Treron calva*, *T.c. ansorgei* is replaced by *T.c. damarensis* along the mid-Okavango. This same pattern is evident in a wide range of other polytypic species, including the woodhoopoes *Phoeniculus damarensis* (in the west) and *P. purpureus angolensis* (in the east), and the Long-tailed Glossy Starling *Lamprotornis mevesii* with *L.m. violacior* and *L.m. benguellensis* in the west and nominate in the east (Clancey 1973). Of moment from the ecological standpoint is the parallel bronzing in the plumages of *P. damarensis* and *L.m. benguellensis*, which are sympatric in the southwest of Angola.

Over the plateau of Zimbabwe and adjacent Mozambique, thence extending on to the littoral plain, is the southeastern terminal block of the Miombo savanna, which is effectively sundered from the main stand lying to the north by the dry Zambezi and Luangwa valleys. This partial isolation is reflected in the presence of a range of Zimbabwean races of species either endemic to or closely associated with the plateau sector of the Miombo savanna. However, in the eastern lowlands the influence of any rivercourse sundering of the environment is minor, as the woodlands are continuous, and, strangely enough, the wide lower reaches of the Zambezi and its flood-plain in Mozambique do not form a functional faunal barrier; more or less continuous populations of a species present both to the north and south of the Zambezi frequently do not differ at all racially. Such influence as the west/east faunal divide of the Rift exerts in the distribution of taxa at this latitude in the Afrotropics also appears circumscribed, except in cases such as the turaco (lourie) forms *Tauraco livingstonii* and *T.(l.) schalowi*, and, again, in the savanna barbets *Stactolaema whytii/sowerbyi*, which may or may not be conspecific, as frequently treated.

It has not been generally appreciated by those interested in zoogeography that the most effective river faunal divide in the southeast of Africa is that furnished by the mid- and lower Limpopo R., reinforced as it is by the eastward extension of the arid climate of the desertic western and interior landmass of the southern parts of the continent. This last is convincingly shown by the finding of discrete races in the east of Sul do Save, southern Mozambique, of such dry country inhabitants as the small granivores: the Shaft-tailed Whydah *Vidua regia* and the Violet-eared Waxbill *Uraeginthus granatinus*.

The localized Miombo subspecies present on the Zimbabwe plateau are in the main restricted distributionally, while those of the same biome



Map 2. The eastern aspects of the Southern African Subregion showing major geographical features alluded to in the general discussion.
1: Rift of Malaŵi (and Shiré R. valley)
2: Lower Zambezi R.
3: Mid-Zambezi R. valley
4: Zimbabwe/Mozambique frontier highlands
5: Save R. (Sabi R. in Zimbabwe)
6: Limpopo R. (and terminal limit of the Miombo savanna)
7: Upper Limpopo R. valley
8: Transvaal Drakensberg Mtns
9: Lake St Lucia region
10: Drakensberg massif
11: Great Fish R.
12: Okavango R.
13: Okavango R. delta and swamp

in the eastern lowlands normally range well to the north of the Zambezi, as in such forms as the Mashona Hyliota *Hyliota australis inornata*, the Red-faced Crombec *Sylvietta w. whytii*, and the Mozambique Batis *Batis soror*. The Save R., interposed in Mozambique between the Zambezi and Limpopo, forms the contact zone between complexes of some polytypic species; among those which may be mentioned are the boubous *Laniarius ferrugineus* and *L. aethiopicus*, and the camaropteras (bleating bush warblers) *Camaroptera brachyura* and *C. brevicaudata* (which hybridize narrowly in the Zimbabwe/Mozambique frontier highlands to the west–Clancey 1970), while genes of *brevicaudata* introgress deeply through the littoral race of the Green-backed Camaroptera *C. brachyura* (*C.b. constans*) to terminate in the northeast of Zululand. The Save valley likewise plays a similar dispositional function in the Black-collared Barbet *Lybius torquatus*, with *L.t. lucidiventris* present to the south of the river and *L.t. vivacens* to the north, the 2 races being part of sequential change from scarlet on the head in the south to creamy or pinkish white to the east of L. Malaŵi, only to revert to bright scarlet again in East Africa in *L.t. irroratus*. It may also be mentioned here that the 2 minor forms of Woodwards' Batis *Batis fratrum* also merge in the Save R. area.

As alluded to earlier, endemics peculiar to the mesic east of southern Africa are relatively few in number. In Zimbabwe only 2 occur. The Boulder Chat *Pinarornis plumosus*, best considered as an integral element of the Miombo avifauna, though confined to rock outcrops and boulder accumulations in the savanna, has a population enclave across the Zambezi in southeastern Zambia and adjacent territories, but no established extant relatives. The second Zimbabwean endemic (and relict) is the so-called Roberts' Prinia *Oreophilais robertsi* of the frontier highlands between Zimbabwe and Mozambique. This is yet another species without established extant allies, which has recently been categorized as belonging to a new monotypic genus (Clancey 1991), having a tail of only 8 rectrices as opposed to the 10 in other long-tailed warblers grouped in the genus *Prinia* Horsfield.

Littoral endemics of the southeast of the Afrotropics south of the Zambezi are Neergaard's Sunbird *Nectarinia neergaardi*, Rudd's Apalis *Apalis ruddi*, the Lemon-breasted Canary *Serinus citrinipectus* and the Pink-throated Twinspot *Hypargos margaritatus*, currently under threat of extinction from the continuing expansion of its close relative *H. niveoguttatus* (see Clancey 1986).

Variation in southeastern humid lowland forms is manifest in increased saturation and lipid levels and a reduction in size, in line with both Gloger's and Bergmann's rules, compared with conspecific races occuring over the interior plateau. Diminution in size not only affects wing- and tail-lengths, but also the mass of the bill in some species, as in 2 small hornbills—the Southern Yellow-billed *Tockus leucomelas parvior* and the Red-billed *T. erythrorhynchus degens*.

The region immediately to the south of the Limpopo R. is, in the east, dominated by the Drakensberg montane system and its complex mosaic of grasslands, intrusive bushveld and patches of evergreen forest, the avifaunal composition of which, as previously asserted, bears the imprint of the major climatic and vegetational vicissitudes of the Quaternary.

Apart from the actual composition of the bird-fauna are the large breaks in the ranges of some widely distributed species, the gaps consisting of stretches of what, to human eyes, is eminently suitable terrain lying untenanted. The reason for this is obscure, but presumably some ancient disruption in the pattern of colonization, or the dying out of populations through competition or local disease may have precipitated it. Such range disruptions are found in the Olive Woodpecker *Mesopicos griseocephalus* and the Plainbacked Pipit *Anthus leucophrys*, and in a rather different version in the 2 white-browed subspecies of the Fiscal Shrike, *Lanius collaris subcoronatus* and *L.c. aridicolus*, of the Southern African Subregion and the isolate *L.c. marwitzi* of southern Tanzania.

The Drakensberg region is the redoubt of a number of small grassland endemics, such as Rudd's Lark *Heteromirafra ruddi*, Botha's Lark *Spizocorys fringillaris*, and 3 or so pipits. Of the latter, the most noteworthy is the Mountain Pipit *Anthus hoeschi*, initially described by Professor Erwin Stresemann in 1938 from the Erongo Mtns of Namibia, where the type-material was taken while the birds were on migration. *A. hoeschi* breeds in the higher and alpine grasslands of the massif of the Drakensberg, spending the non-breeding season in the Zambezi/Zaïre watershed. Rudd's Lark and another of the pipits—the Yellow-breasted *Hemimacronyx chloris*—have spatially remote congenerics in East and northeastern Africa. The Drakensberg area also boasts of a range of endemic turdines, such as the Buff-streaked Chat *Campicoloides bifasciatus*, which has no extant relatives (Clancey 1990), and 2 rockthrushes *Monticola* spp., deriving from old colonisations by Palaearctic ancestors. Among non-passerine endemics, also relevant are the Bald Ibis *Geronticus calvus* and the small bustards *Eupodotis caerulescens* and *E. afraoides*.

Of biogeographical import is the limited range of endemics confined to stands of evergreen forest present locally over the southeastern highlands and southern mountains (see Clancey 1986), notable among which are the Southern Mountain Buzzard *Buteo trizonatus*, the Knysna Lourie *Tauraco corythaix* and the Bush Blackcap *Lioptilus nigricapillus*, amongst others. Regarding subspeciation, it is worthy of note that in some characteristic forestal species, southern populations have diversified from restriction to a forest environment and now exploit niches in both mesic and xeric habitats, this translating into the development of dry country subspecies. Such birds are the Olive Thrush *Turdus olivaceus* (with the xeric *T.o. smithi* nearing the level of a full species), the Cape Robin *Cossypha caffra* and the small Lesser Double-collared Sunbird *Nectarinia chalybea*, the extralimital parts of their ranges being tenuous and fragmented compared with what is found in the south of the continent. In the sunbird, close analogues in the sub-genus *Cinnyris* replace it to the north of the Limpopo R. (Clancey & Irwin 1978, Clancey 1986).

What may be referred to as the terminal avifaunal division of the Afrotropics, namely the Winter Rainfall District of the Cape, supports a limited number of endemics restricted to the Cape Fynbos (Macchia) biome, dominated by *Protea* and heath *Erica* spp. Among these are the Cape Sugarbird *Promerops cafer* referred to earlier, Victorin's Scrub Warbler *Bradypterus victorini*, the Orange-breasted Sunbird *Nectarinia violacea*, the Protea Seed-eater *Poliospiza leucoptera* and the Cape Siskin *Pseudochloroptila totta*. The entire region is relatively constricted, being centred on the mountains (and then largely on their seaward facing versants) lying to the south of the South West Arid Zone from the Cape of Good Hope, eastwards to just west of Algoa Bay. Taxonomically relevant variation in local polytypic bird species differs little from that defined above for those present in the east of southern Africa, but on the whole shows an inclination towards a still more saturated and heavily marked dorsal and ventral plumage. Variation in size is limited, but, as shown earlier, can affect bill-mass, as in the bishop *Euplectes capensis*.

AVIAN CLINES IN SOUTHERN AFRICA

The cline concept as initially proposed by J. S. Huxley (1939) has frequently been misapplied in avian systematics, consistently so by some authors who have found its use advantageous in the disposing of otherwise intractable problems encountered in research into geographical variation.

In the southern third of Africa variation interpretable as clinal *sens. strict.*, is to be found in remarkably few birds. Those so affected are largely centred on arid country, the biota of which, as demonstrated earlier, was much less affected by the disruptive events of the Quaternary. In the case of the mesic north and in the east and south, clinal variation has not been found in the many (polytypic) species closely studied in recent years, this finding being a result of the periodically disrupted pattern of faunal augmentation which characterizes the regions' immediate past history.

Amongst the species of the Arid Zone, mensural variation, which is indubitably clinal in form, affects few species, the most notable of which is the Pale-winged Starling *Onychognathus nabouroup*, an endemic extending narrowly from coastal desert Angola to the Karoo of the Cape, where it meets and interdigitates with the nominate race of the Red-winged Starling *O. morio*. In *nabouroup*, size reaches its maximum in the southern Karoo, declining northwards through Namibia to terminate in southwest Angola, the size gradient not being visibly stepped at any point. However, the starkly whiter webs of the remiges of the northern desertic populations (*O.n. benguellensis*) in newly moulted condition can be invoked in the upholding of the 2 subspecies accepted by most workers (*pace* Craig 1988). In a second case, the extensive range of the nominate subspecies of the Short-toed Rockthrush *Monticola brevipes* extends from the mid- and lower reaches of the Orange R. through Namibia to the coastal desert of Angola. The northern populations of *M.b.brevipes* average slightly paler than the southern ones, while the males of the Angolan coastal deme frequently display a pale central chin-stripe. Study, however, has indicated that subdivision of the nominate race is not justified, as the colour transition is essentially clinal and too slight to warrant nomenclatural recognition, and as for the chin-stripe in males, its limited occurrence in the Angolan coast series available does not merit its use. Accordingly, the proposed northern minor race of *M.b. kaokoensis* is not currently recognised and is treated as part of nominate *brevipes*.

A great measure of so-called clinal colour-variation in dry country birds with an extensive continuum of populations in a continental land-mass is in the form of stepped yet graded mosaic-like progressional change involving either single or combinations (suites) of variables. A tendency to form a clinal disposition may only affect a lone variable in a species and not the other characters. The patterns are normally closely concordant with local precipitation or vegetational (major biome) contouring, and are phenotypically correlated as a result. As mentioned earlier, in the arid country and its periphery, steps and local disruptions in the various character gradients allow of the recognition of some 3–4 subspecies in moderately polytypic species, the pattern being dark in the south and southeast to a pale extreme in close association with almost absolute desert in the northwest. Size shifts pursue a closely similar pattern, with large elements in the cooler south and smaller sized ones in the northwest. Dismissal of variation as simply clinal, thus denying it any formal taxonomic recognition, is frequently based on study of severely limited material, too often collected in a narrow zone of secondary intergradation or on the step of a gradient. Such, assuredly, does not fulfil the scientific requirements needed for the determination of a true cline as envisaged by Huxley.

SOUTHERN AFRICAN PRIMARY AND SECONDARY CONTACT ZONES

In relation to the above issues, the resident bird fauna of the areas of Africa lying to the south of the Limpopo and Orange Rivers furnishes a lucrative field for investigative research. In his highly instructive paper on hybrid (contact) zones in Australian birds, the late Julian Ford (1987) describes them in his 'Introduction' as "regions of steep genetic and phenotypical intergradation between relatively uniform contiguous populations", going on to state that morphological change across geographical fronts may arise locally through selection by an environmental gradient without the involved populations having been previously isolated. As a result primary and secondary contact zones may be difficult to distinguish. The following includes only some of the contact zones identified more recently in southern Africa.

The White-eye *Zosterops* spp. complex resident in the south of and to the south and east of the South West Arid Zone has, in the western populations in which the ventral yellow is restricted to the throat and under tail-coverts, the mid-ventral surface white tinged laterally with buff or grey. To the east of these elements occur 2 plexuses of birds with the entire under-parts yellow. One of these is morphologically part of the western oriented *Z. pallidus* (the subspecies *Z.p. virens* and *Z.p. caniviridis*), while the other is part of *Z. senegalensis*, which lies spatially removed from *Z.p. virens* and *caniviridis*, though just impinging on the former in lowland Zululand. These last mentioned 2 forms hybridize in depth in a contact zone over the Drakensberg Mtns with the western white-bellied forms. This contact zone derives from an earlier invasive thrust by an ancestor of *senegalensis*, the descendants of which in contemporary mode furnish, as stated, a further secondary but largely detached convergence on the southern African endemic complex of *Z. pallidus*.

An instructive mosaic of secondary contacts between close congenerics is that of the tightly-knit South African ranges of *Pycnonotus capensis*, *P. nigricans* and *P. barbatus*, with only limited hybridization between the individual paraspecies at points along their range interfaces. An analogous combination is also furnished by the batis forms *Batis pririt*, *B. molitor* and *B. soror*, which range within current limits from Namibia and the Cape east to Mozambique, replacing one another parapatrically without hybridization where their ranges converge. *B. soror* is a Miombo savanna monotypic endemic, whereas *pririt* and *molitor* are polytypic species of *Acacia* and bushveld savanna woodlands. Here, it is worth pointing out again the hybridizing of the *Camaroptera* spp. forms in the upper Save (Sabi) R. drainage; and allude to the hybridization between the parrots *Poicephalus cryptoxanthus* and *P. meyeri* from southeastern Zimbabwe to the northeastern Transvaal and adjacent Mozambique (see Clancey 1977). This latter case is of significance as *meyeri* does not hybridize with its western allospecies *P. rueppellii* in Namibia. Among the austral African larks one finds a particularly interesting instance in the Dune Lark *Certhilauda erythrochlamys* of the dunes of the Namib Desert in Namibia, which at some stage expanded its range into the extremely arid lower Orange R. basin. The subspecies (or near species) so formed, namely *C.(e.) burra*, the so-called Red Lark, now hybridizes on its range periphery with the Karoo Lark *C. albescens*, which latter even intrudes between *burra* and the Namibian forms of *erythrochlamys* (see Clancey 1989b).

A re-examination of the variation in the southern populations of the Cape Turtle Dove *Streptopelia capicola* (Clancey 1989a) determined that 2 of the local races were derived from longstanding and now consolidated hybridizing events, both races being distinguishable from either of the parental forms.

In the subspecific interpretation of variation in the Ground Woodpecker *Geocolaptes olivaceus* mentioned earlier, this resulted from early splitting of populations between western and eastern faunal refugia, occasioned by the spread of aridity during the Quaternary. The descendants now meet in a broad zone of secondary contact in the eastern Cape.

In cases of what is in effect secondary contact, the contending taxa may not necessarily be physically contiguous, being segregated by an intrusive stretch of untenanted terrain, well shown in the range map of the 2 allospecies of Black Korhaans *Eupodotis afra* and *E. afraoides* (see Clancey 1989). In such cases it seems as if the descendants of the initial colonization have withdrawn in the face of the expanding and dynamic secondary colonist. On the other hand, such a range hiatus may have resulted from selection against the resulting hybrids from direct physical contact at an early stage. Further and more detailed investigative research into this detached form of contact by closely allied taxa, of which several others have so far been identified, may help shed some additional light on the possible evolutionary mechanisms involved in their formation.

CONCLUSIONS AND SUMMARY

The Southern African Subregion with its involved mosaic of mesic habitats distributed to the north, east and south of an extensive arid zone, which varies from dry savanna and steppe-like conditions to near absolute desert along the western seaboard, supports a large and varied avifauna, of which some 70% of the 170 determined endemics of the entire subregion are peculiar to the arid sector, namely the South West Arid Zone. Many of these have radiated subspecifically in response to the long-term environmental stasis of this dry region. The mesic environments arcing round this arid sector have by contrast many fewer endemic species; yet the mesic avifauna is both integrally varied and rich. The

TABLE 1
Subspeciation in some Southern African Subregion families

Family	Total of species	No. of subspecies	No. of monotypic species	No of taxa below generic level
Phasianidae	15	39	1	40
Otididae	11	14	3	17
Columbidae	13	30	nil	30
Lybiidae	10	23	nil	23
Picidae	9	25	nil	25
Alaudidae	23	92	6	98
Turdidae	40	97	8	105
Sylviidae (excluding the Cisticolidae)	42	123	2	125
Sturnidae	12	17	2	19
Fringillidae (genera *Serinus* and *Poliospiza*)	12	35	3	38

Note. Comparable data for other families can be computed from the *S.A.O.S. Checklist of Southern African Birds* (Clancey 1980) and the revisionary updates of 1987 and 1991.

comparative shortfall in endemic species is a result of the major climatic and vegetational events of Quaternary times.

The magnitude of the resident bird fauna of the Southern Afric-Subregion and its wide range of environments translate into a wealth of subspeciation, as shown in examples in Table 1. Comparable data for other families can be computed from the *S.A.O.S. Checklist of Southern African Birds* (Clancey 1980) and the revisionary updates of 1987 and 1991.

Clines (*sens. strict* Huxley 1939) affecting both mensural and colour variables have been found to be limited in the avifauna present south of 16° S in Africa, and restricted to the South West Arid Zone. No cases have been found among residents in the various mesic vegetational types distributed peripherally to the arid country, assuredly due to the fundamental climatic shifts during the Quaternary and attendant subsequent vegetational and other ecological changes.

Variation, often interpreted as on a cline, may, on critical study, be found to consist of a suite of variables rather than a single one, and disposed mosaically through the entire plexus of populations. In such instances, a clinal style of progressional character shift will normally only affect a single criterion, which, unless stepped at some point, may be disregarded for formal taxonomic purposes.

In examples of primary and secondary contact zones south of 16° S, most of them researched in depth, so far occur in the southeastern lowlands, with some clearly linked to the termination of the *Julbernardia*/*Brachystegia* (Miombo) savanna on the Limpopo. Most are seemingly cases of primary contact. The Cape Province boasts of a range of secondary contacts, as in the Ground Woodpecker *Geocolaptes*, while among the 3 *Pycnonotus* bulbuls, the paraspecies clearly furnish an example of secondary contact with minimal hybridization at the interfaces of the ranges. In yet other instances, the taxa are in close geographical but not direct physical contact, and are effectually allospecies, narrowly segregated from one another by untenanted country. The reasons underlying this latter aborted type of contact are as yet only speculative.

References:

Clancey, P. A. 1970. Comments on some anomalous Bleating Bush Warblers from eastern Rhodesia. *Durban Mus. Novit.* 8(17): 335–337.
— 1973. A new race of *Lamprotornis mevesii* (Wahlberg) from north-western South-West Africa and adjacent Angola. *Durban Mus. Novit.* 9(18): 279–283.
— 1977. Variation in and the relationships of the Brownheaded Parrot of the Eastern African Lowlands. *Bonn. Zool. Beitr.* 28(3/4): 279–291.
— (Ed.) 1980. *S.A.O.S. Checklist of Southern African Birds*. Southern African Ornithological Society, Johannesburg.
— 1985. Species limits in the Long-billed Pipits of the southern Afrotropics. *Ostrich* 56: 157–169.
— 1986. Endemicity in the Southern African avifauna. *Durban Mus. Novit.* 13(20): 245–284.
— 1986a. Further comment on variation in the Afrotropical Redeyed Dove *Streptopelia semitorquata* (Rüppell), 1837. *Durban Mus. Novit.* 14(2): 9–13.
— 1988. Variation in the Ground Woodpecker *Geocolaptes olivaceus*. *Bull. Brit. Orn. Cl.* 108(2): 93–98.
— 1989. Four additional species of southern African endemic birds. *Durban Mus. Novit.* 14(7): 140–152.
— 1989a. The status of *Streptopelia capicola onguati* Macdonald, 1957. *Bull. Brit. Orn. Cl.* 109(4): 225–227.
— 1989b. Taxonomic and distributional findings on some birds from Namibia. *Cimbebasia* 11: 111–133.
— 1990. The generic status of the Buff-streaked Chat of the Southern Afrotropics. *Le Gerfaut* 80: 179–186.
— 1991. The generic status of Roberts' Prinia of the south-eastern Afrotropics. *Bull. Brit. Orn. Cl.* 111(4): 217–222.
Clancey, P. A. & Irwin, M. P. S. 1978. Species limits in the *Nectarinia afra/N. chalybea* complex of African doublecollared sunbirds. *Durban Mus. Novit.* 11(20): 331–351.
Craig, A. J. F. K. 1988. The status of *Onychognathus nabouroup benguellensis* (Neumann). *Bull. Brit. Orn. Cl.* 108(3): 144–147.
Earlé, R. A. 1986. Reappraisal of variation in the Ground Woodpecker *Geocolaptes olivaceus* (Gmelin) (Aves: Picidae) with notes on its moult. *Navors. Nas. Mus. Bloemfontein* 5(7): 79–92.
Ford, Julian, 1987. Hybrid Zones in Australian Birds. *Emu* 87: 158–178.
Hoesch, W. & Niethammer, G. 1940. *Die Vogelwelt Deutsch-Südwestafrikas. J.f. Orn.* 88, Sonderheft.
Huxley, J. S. 1939. Clines: an auxiliary method in taxonomy. *Bijdr. Dierk.* 27: 491–520.

Note: An extended list of additional references dealing with subspecific variation and particularly endemicity in southern African birds may be found in Clancey (1986).

Address: Dr P. A. Clancey, Research Associate, Durban Natural Science Museum, P.O. Box 4085, Durban 4000, South Africa.

© British Ornithologists' Club 1992

Myrmecophagy by *Pseudochelidon eurystomina* and other African birds

by C. H. Fry

Received 10 March 1992

Feeding upon dangerously venomous prey such as Hymenoptera, scorpions and snakes must present birds with problems, the adaptive morphological and physiological solutions to which have not received a great deal of attention from ornithologists. Although ants (Formicidae), some other hymenopterans, and termites (Isoptera) are abundant in humid regions, birds that exploit them for food incur a further set of problems arising from their prey's swarming and patchy distribution. Some aberrant social and behavioural adaptations of such specialist bird species are already known and more may be expected to be found. For both reasons, physiological and sociobiological, myrmecophagy or ant-eating by birds should be of interest. This paper adds a swallow to the known 'professional' myrmecophages amongst African birds, and briefly reviews ant predation in African nonpasserine and several passerine families.

Pseudochelidon eurystomina

The African River Martin *P. eurystomina* is an aberrant swallow or swallow-like bird generally placed in the hirundine subfamily Pseudochelidoninae, of which the only other species is *P. sirintarae*. The latter was discovered in 1968 and is known only from the few birds that wintered at Bung Boraphet reservoir in central Thailand 1968–1980; it has not been seen since (Turner & Rose 1989). Chapin (1953) provided the basis of knowledge about *P. eurystomina*, about which rather little is still known (Keith *et al.* 1992), although further observations have recently been made at a breeding colony near Animba, Port Gentil (0°58′S, 8°54′E), Gabon, September–October 1989 (Alexander-Marrack, in press). Its known breeding range is the middle and upper Congo River and the lower Oubangui River where it occurs from January to April-May, and near the coast of Gabon and Congo Republic where it occurs only from May/June to November, breeding September–October. There is some evidence of migration between the interior and coastal regions (Erard 1981).

The species is thought to forage exclusively on the wing, and its flight actions are reminiscent more of American *Progne* martins than of typical *Hirundo* swallows. Dense flocks fly with the co-ordinated precision of European Starlings *Sturnus vulgaris* (Brosset & Erard 1986); almost nothing else is known about the social organization of this swallow.

Materials and methods

P. Alexander-Marrack made a small collection of faeces and regurgitates (pellets) at the Animba colony and enabled me to examine them.

TABLE 1.
Prey of *Pseudochelidon eurystomina*, Animba, Gabon, 1989: (a) faeces, 24 September, (b) regurgitates, 1 October, (c) regurgitates, 15 October

	(a)	(b)	(c)	Totals	%	Approx. no. of genera
Odonata	0	3	4	7	0.7	2
Isoptera	39	198	6	243	23.8	2
Heteroptera	1	1	1	3	0.3	3
Lepidoptera	0	1	0	1	0.1	1
Diptera	4	0	0	4	0.4	3
Neuroptera	0	0	1	1	0.1	1
Coleoptera	1	2	8	11	1.1	5
Formicidae	49	225	387	661	64.8	17
Other Hymenoptera	1	73	15	89	8.7	32
Totals	**95**	**503**	**422**	**1020**	**100.0**	**66**

Faeces are straight or curved cylinders 2.0–3.2 mm in diameter, found in pieces up to 9 mm long, consisting of densely-packed blackish sclerites in a sleeve of white crystalline uric acid. They were teased by hand and heated to 40°C in glycerol for 5 hours to dissolve the uric acid. Insect head capsules, mandibles, wings and some other recognizable fragments were sorted by hand and identified taxonomically by reference to the literature and insect collections at Sultan Qaboos University, Oman. Apart from loss of antennae, setae and some mouthparts, head capsules were rarely damaged; many even retained antennae and all mouthparts.

The regurgitates consisted of 10–12 ovoid or subspherical dry blackish pellets measuring 6–7 × 10–11 mm, and together weighing 1.4 g. They were moistened with ethanol and divided into 26 subsamples which were teased and sorted by hand in ethanol using a high-powered dissecting (binocular) microscope. After removal of insect head capsules, 5 subsamples were re-examined and the number of further head capsules recovered indicated that at least 95% of them had been recovered in the initial search.

Results

Regurgitates and faeces consist entirely of insect remains. More than 1000 head capsules were recovered, in proportions of taxa that differed substantially between the 3 samples (Table 1). In total, ants compose about 65% of the diet of *P. eurystomina*, other hymenopterans 9%, termites 24%, and all other insect Orders only about 2%. A few almost entire ants present in pellets were identified from keys in Hölldobler & Wilson (1990) as species of *Camponotus* (Formicinae) and *Crematogaster*, *Monomorium* and *Pheidole* (Myrmicinae). Other ants were not identified to genera. At least 17 types or genera of ants were evident in the samples, but many of the 32 apparent taxa and 89 specimens of 'other Hymenoptera' may well have been ants also, to judge from descriptions of head capsules in Hölldobler & Wilson. 29% of the ants appeared to belong to a single (unidentified) taxon and 43% to 5 others.

Six whole ants were 6, 6, 7, 8, 9 and 10 mm long. Widths of ant head capsules, in relation to the head size and body lengths of the whole ants, suggested that the majority of ant prey were *c.* 8 mm long. Largest prey items were a damselfly (Odonata) probably >30 mm long and a sphecid wasp probably 13–16 mm long. At the other extreme, some hymenopteran heads were only 0.3 mm in width so that the whole insect may have been no more than 2 mm long; and an entire beetle was only 2.2 mm long.

Predation on ants by African birds

Information on diets of birds in Africa has been obtained mainly by museum skin collectors, economic biologists studying waterfowl, gamebirds and agricultural pests, and ornithologists reporting on gizzard contents of road kills or analysing regurgitated pellets. The literature, which is large and diffuse, has been reviewed in *The Birds of Africa* (Vols 1–4: Brown *et al.* 1982, Urban *et al.* 1986, Fry *et al.* 1988, Keith *et al.* 1992), with accounts of 1187 species, including all of the nonpasserines and the passerines from Eurylaimidae to *Myrmecocichla* in Turdidae. There are *c.* 864 remaining passerines (*Monticola, Zoothera, Turdus*, warblers, flycatchers, sunbirds, shrikes, starlings, weavers, finches etc.), for which no data have been collected, and to that extent this review and Table 2 are incomplete. Neither primary literature sources, nor such essentially extra-African works as *The Birds of the Western Palearctic* (see especially Vol. 5, Cramp 1988), have been utilized. In the latter work, food data from Africa for species that visit or reside there are summarized in *The Birds of Africa*; food data from Europe are somewhat peripheral to this paper and in general have been ignored. Many taxa are not implicated in ant-eating at all: they are listed in the Appendix and, excluding 194 fully aquatic foragers, they represent 359 species.

Table 2 lists 116 genera, each with one or more species that eat ants. The genera include 622 African species, of which 272 eat ants—that is 28% of the terrestrial avifauna (359+622 species) reviewed to date. It is likely that most congeners of ant-eating species will eventually be found to eat ants also, occasionally if not regularly. In that event the proportion of myrmecophagous species in the terrestrial avifauna could prove to exceed 60%.

Major ant predators

Fifty-five species are identified as major ant predators in Table 2 (quotations are from *The Birds of Africa*).

PHASIANIDAE *Alectoris barbara*: "Seeds, fruits and leaves, supplemented by insects, especially ants . . . food of young often mainly ants". *Francolinus lathami*: "90% arthropods, especially termites *Basidentitermes* spp. and ants *Psalidomyrmex* spp.". *F. levaillantii*: 70–80% of the crop volume is vegetable matter, and the rest of the diet is "mainly ants, spiders, grasshoppers, millepedes and beetles". *F. capensis*: vegetable matter and "insects (especially termites and ants)". Phasianids in general and francolins *Francolinus* in particular appear to be important ant predators.

TABLE 2.
Genera and numbers of species of African birds known to eat ants
(from *The Birds of Africa* 1–4)

Family and genus	Numbers of species in Africa	known to eat ants	major ant predators	Family and genus	Numbers of species in Africa	known to eat ants	major ant predators
			NON-PASSERINES				
THRESKIORNITHIDAE				**CAPRIMULGIDAE**			
Threskiornis	1	1		*Caprimulgus*	21	7	
Geronticus	2	1		*Macrodipteryx*	2	2	
PHASIANIDAE				**APODIDAE**			
Agelestes	2	1		*Rhaphidura*	1	1	
Guttera	2	1		*Telecanthura*	2	2	
Numida	1	1		*Neafrapus*	2	2	
Coturnix	3	2		*Schoutedenapus*	2	1	
Alectoris	2	1	1	*Cypsiurus*	1	1	
Francolinus	36	8	3	*Apus*	11	8	
TURNICIDAE				*Tachymarptis*	2	2	
Turnix	2	1		**COLIIDAE**			
RALLIDAE				*Colius*	4	1	
Himantornis	1	1		**ALCEDINIDAE**			
Canirallus	1	1		*Halcyon*	9	2	
Sarothrura	7	3		**MEROPIDAE**			
Crex	2	2		*Merops*	18	10	3
OTIDIDAE				**CORACIIDAE**			
Neotis	4	2		*Coracias*	6	3	
Chlamydotis	1	1	1	*Eurystomus*	2	2	2
Eupodotis	9	2		**PHOENICULIDAE**			
GLAREOLIDAE				*Phoeniculus*	8	5	
Cursorius	6	1		**UPUPIDAE**			
Glareola	5	1		*Upupa*	1	1	
CHARADRIIDAE				**BUCEROTIDAE**			
Vanellus	14	5		*Tockus*	14	6	
LARIDAE				*Ceratogymna*	7	4	
Larus	20	3	1	**CAPITONIDAE**			
Chlidonias	3	1		*Stactolaema*	4	1	
PTEROCLIDAE				*Pogoniulus*	10	1	
Pterocles	12	1		*Tricholaema*	6	1–2	
COLUMBIDAE				*Lybius*	12	3	
Streptopelia	11	1		*Trachyphonus*	5	2	
CUCULIDAE				**INDICATORIDAE**			
Cuculus	6	1		*Indicator*	9	6	
Cercococcyx	3	1		**PICIDAE**			
Centropus	7	2		*Jynx*	2	2	2
STRIGIDAE				*Campethera*	10	10	10
Glaucidium	5	1		*Geocolaptes*	1	1	1
				Dendropicos	12	4	
				Picoides	3	1	
				Picus	1	1	1

Continued on next page

TABLE 2. *(cont.)*.

Family and genus	Numbers of species in Africa	known to eat ants	major ant predators
PASSERINES			
PITTIDAE			
Pitta	2	1	
ALAUDIDAE			
Mirafra	21	3	1
Certhilauda	5	4	2
Pinarocorys	2	1	
Chersomanes	1	1	
Alaemon	2	1	
Rhamphocoris	1	1	
Ammomanes	3	2	
Calandrella	4	3	
Spizocorys	5	1	
Eremalauda	2	1	
Chersophilus	1	1	
Galerida	4	3	
Eremopterix	6	2	
HIRUNDINIDAE			
Pseudochelidon	1	1	1
Psalidoprocne	5	3	
Riparia	4	1	
Hirundo	24	9	3
Delichon	1	1	
MOTACILLIDAE			
Motacilla	6	3	
Anthus	19	1–3	1
Macronyx	8	1	
CAMPEPHAGIDAE			
Coracina	4	1	
PYCNONOTIDAE			
Andropadus	11	5	
Baeopogon	2	1	
Ixonotus	1	1	
Thescelocichla	1	1	
Phyllastrephus	17	5	1
Bleda	3	3	
Criniger	5	1	
Pycnonotus	4	2	
TURDIDAE			
Pogonocichla	1	1	1
Swynnertonia	1	1	1
Stiphrornis	1	1	
Sheppardia	8	4	
Erithacus	1	1	1
Luscinia	3	3	
Irania	1	1	
Cossypha	14	9–10	6
Xenocopsychus	1	1	
Alethe	5	5	1
Neocossyphus	4	4	1
Cercotrichas	10	8	4
Namibornis	1	1	
Phoenicurus	3	3	1
Saxicola	3	2	
Oenanthe	17	16	3
Cercomela	8	1	
Myrmecocichla	9	5	2

OTIDIDAE *Chlamydotis undulata*: vegetable matter, "small invertebrates especially ants and beetles, and small reptiles".
CHARADRIIDAE Lapwings *Vanellus* probably eat significant amounts of ants.
LARIDAE *Larus audouinii*: "Of 120 Apr–June pellets from Morocco, 87% contained fish, 5% insects . . . insects were winged ants (40%)".
CAPRIMULGIDAE Of 23 nightjar species, 9 are known to eat alate ants, of which these birds are probably major predators.
APODIDAE Of 21 species, no less than 18 eat ants, and swifts are probably even more important myrmecophages than nightjars.
MEROPIDAE 10 out of 18 African bee-eaters consume ants. *Merops albicollis*: Nigerian pellet samples "(n = 1700 insects) were . . . ants (overall 56%)" and Ivory Coast gizzards "(n = 1500 insects) were 55% ants (1 gizzard with 200 *Crematogaster* ants). Flying termites not commonly eaten". *M. orientalis*: "Airborne insects: 75% Hymenoptera . . . mainly ants". *M. malimbicus*: "Flying ants (70% of 1250 prey items,

R. Niger)". Further details of ant-eating in African bee-eaters are given by Fry (1984).

CORACIIDAE *Coracias* rollers may be important predators of ants, but, certainly, few African genera are more so than the broad-billed rollers *Eurystomus*. *E. gularis*: "Flying ants (91% of 3623 items in 20 stomachs, mainly *Crematogaster*, also *Oecophylla*), flying termites 3%". *E. glaucurus*: "Specialises on swarming winged ants (e.g. *Crematogaster, Oecophylla*) and termites (e.g. *Macrotermes, Pseudacanthotermes*). 1644 insects from stomachs were: ants 66%, termites 15%". "Up to 280 birds quickly assemble at a large hatch and feed . . . with swifts and swallows . . . [each catching] 6–10 [insects] per min . . . normally 200–400 and sometimes 600–800 insects" (Thiollay 1970).

BUCEROTIDAE and CAPITONIDAE Ground- and tree-feeding hornbills (*Tockus, Ceratogymna*) and ground-feeding barbets (*Trachyphonus*) may be major ant predators.

PICIDAE Both species of wrynecks, *Jynx*, all 10 species of the endemic woodpecker genus *Campethera*, the ground woodpecker *Geocolaptes olivaceus*, and the only African species of *Picus*, are predominantly myrmecophages. *Jynx torquilla*: "Mainly ants, up to 500 reported in 1 stomach . . . young fed on adults, pupae, larvae and eggs of ants." *J. ruficollis*: "Mainly ants, their larvae, pupae [and] eggs . . . from ant nests in the ground, also on trees . . . the small ants *Pheidole megacephala* and *Crematogaster castanea* made up *c*. 88% of diet (Tarboton 1976)". *Campethera punctuligera*: "Stomachs (n = 25) contained only ants, their larvae and pupae, and in 5 cases, termites". *C. abingoni*: "Almost entirely ants, their pupae, larvae and eggs". The other *Campethera* species are reported in like vein, although their diets are less well known. *Geocolaptes olivaceus*: "Entirely ants (pupae, larvae, eggs, adults) of various unidentified spp.". *Picus viridis*: "Major food, ants (*Camponotus nylanderi, Crematogaster scutellaris*)".

ALAUDIDAE Six lark genera are not yet known to eat ants in Africa; 13 genera are known to, and of their 57 species, 24 (42%) take ants and 3 or more could be major predators. *Mirafra apiata*: "Ants . . . and . . . termites (*Hodotermes mossambicus*)". *Certhilauda curvirostris*: "Insects (termites, including *Microhodotermes viator* . . . ants *Tetramorium* and *Anoplolepis*)". *C. albescens*: ants include *Messor, Pheidole, Tetramorium, Crematogaster* and *Acantholepis*. *Chersomanes albofasciata*: "Insects. ♂♂ eat more tenebrionid beetles, ♀♀ more ants and harvester termites". *Spizocorys sclateri*: invertebrates—caterpillars, small beetles, "ants (*Messor capensis, Monomorium* spp.)".

HIRUNDINIDAE Like other small-billed aerial insectivores (nightjars, swifts), most swallows almost certainly consume large numbers of ants in Africa as they are known to do elsewhere (Turner & Rose 1989). Detailed investigations of most species have been lacking in Africa. An exception is *Hirundo spilodera*, in which the main prey are beetles, flies and wasps. Ten species of ants occurred in 4–16% of stomachs (genera *Simonopone, Messor, Pheidole, Solenopsis, Tetramorium, Triglyphothrix, Anoplolepis, Camponotus*) and *Camponotus maculatus* occurred in 36% of another sample (Earlé 1985). Diets of the swallows *Phedina* and *Pseudhirundo* are unknown; the 5 other genera all catch ants, and of their 35 species at least

15 (43%) do so. Major predators are *Pseudocalyptomena eurystomina*, whose diet is 65% ants, 8% other hymenopterans and 24% termites, and 2 more species of *Hirundo*. *H. daurica*: "Not studied in Africa, but in France 25-day nestlings were fed 255 items, 94% winged ants". *H. rustica*: food in Africa is very varied and includes arillate seeds. Ants feature as follows: "Small airborne insects, mainly ants, flies and beetles (25 birds, Uganda) . . . 4 birds, Orange Free State, each contained 17–120 ants [only] . . . 2 road kills, Kenya, contained . . . 22 winged ants [and 43 other insects] . . . casualties at a Zimbabwe roost had stomachs packed solid with small flying ants".

MOTACILLIDAE *Anthus cervinus*: "Insects and their larvae (especially ants, beetles, flies)".

PYCNONOTIDAE 19 out of 44 species in 8 genera are known to eat ants and 3 other genera are not yet implicated. *Andropadus* and *Phyllastrephus*, with 5 ant-eating species each, may be important. All 3 *Bleda* species eat ants. *P. terrestris*: "Arthropods, including insects . . . especially ants".

TURDIDAE Of the 26 African genera, only 3 (*Monticola, Zoothera, Turdus*) have not been dealt with in *The Birds of Africa* so far. Five of them are not yet known to eat ants: *Cichladusa* (with 3 species) and the monotypic *Cossyphicula, Modulatrix, Arcanator* and *Pinarornis*. Of the other 18 genera, 67 of their 91 species (74%) take ants, and 21 or more species are major predators. The endemic alethes *Alethe* habitually attend army ant swarms in forest; the 5 *Alethe* species eat some army ants (*Dorylus*), but they depend mainly on other invertebrates that the army ant columns flush. Some species of *Neocossyphus* are known as ant-thrushes and some of *Myrmecocichla* as anteater-chats, with good reason. Robins, and robin-chats *Cossypha*, are particularly important ant predators (Oatley 1970, 1992). *Pogonocichla stellata*: ants were found in 43% of faecal samples in Natal (but were outnumbered by moths and particularly beetles). *Swynnertonia swynnertoni*: "In 25 stomachs and 4 faeces (Chirinda, Zimbabwe), there were beetles in 93%, ants in 55% . . . In 20 [other] stomachs, beetles and ants made up 72%". *Erithacus rubecula*: food in North Africa has not been studied but in south Spain in one study "of >1900 invertebrates 76% by number were ants". *Cossphya caffra*: in 104 samples mainly from Natal "ants occurred in 88%". *C. humeralis*: in 38 samples "there were beetles in 63%, ants in 55%"; this robin-chat also eats termites, spiders, fruits, etc. *C. heuglini*: in 28 samples from Zaïre, Zambia, Malaŵi and Zululand there were "ants (Ponerinae, Dorylinae, Camponotinae, Myrmicinae) in 86%". *C. natalensis*: in 47 samples from 5 countries there were "beetles . . . in 79%, ants in 77%" and smaller percentages of other invertebrates and fruits. *C. dichroa*: in 44 samples "from Natal and Transvaal there were beetles in 73%, ants in 61%, moths and caterpillars in 34%" etc. *C. heinrichi*: "Principally ants, including doryline driver ants". *Alethe poliophrys*: "Insects, including beetles, flies and army ants (60–80 in one stomach . . .)". *Neocossyphus poensis*: "insects, larvae and pupae (ants, including army ants; termites, beetles, grasshoppers)". *Cercotrichas quadrivirgata*: in 21 samples from Malaŵi and Natal there were beetles in 76%, ants in 71%, termites in 48%, etc. *C. signata*: analysis of 27 samples showed that "ants (63%), beetles (59%), and millipedes (48%) are the most frequent prey". *C. leucophrys*: in 51 "samples from southern Africa there were: termites in 69%, ants in 67%, beetles . . . in 59%", etc. *C. paena*: "In 8 stomachs (Botswana, Transvaal) there were: termites . . . in 100%, beetles . . . in 62%, ants (Ponerinae, Myrmicinae) in 62%", etc. *Phoenicurus moussieri*: "Insects, mainly ants, beetles, grasshoppers and larvae". Although all but one of the 17 wheatears *Oenanthe* in Africa are known to eat ants, there are few quantitative data and only 3 species seem to be major predators of ants. *Oenanthe leucura*: "Mainly insects, especially beetles and ants". *O. lugens*: "Mainly ants; also beetles, grasshoppers and other insects". *O. pileata*: "Insects, especially ants, also flies, locusts", etc. *Myrmecocichla formicivora*: "Insects, especially ants and termites. In 33 birds near Bloemfontein, South Africa, Hymenoptera (almost all Formicidae) dominated numerically in summer, and they and termites (entirely *Hodotermes*) in winter" (Earlé & Louw 1988). (The diet of *M. aethiops*, the Northern Anteater-Chat, has not been quantified; it is doubtless much like its allospecies *A. formicivora*.) *M. arnotti*: "Insects and spiders, especially ants".

Discussion

Chapin (1953) reported that *Pseudochelidon eurystomina* feeds entirely on the wing and that stomachs contained a few Hemiptera, Homoptera, beetles, flies and small butterflies, and many alate ants. Recent observers also report that this aberrant swallow forages largely if not exclusively in flight; and Chapin's early diagnosis about its diet is amply confirmed by the present study.

Ants are an abundant, diverse, and conspicuous component of the tropical insect fauna, in savanna grassland and woodland as well as in rainforest. It is thus not altogether surprising to find that 28% (and possibly >50%) of the terrestrial bird fauna exploit them. However, it is remarkable that as many as 55 species appear to be specialist myrmecophages, a number that can only rise when information on the 864 uninvestigated passerines becomes available.

Major ant predators fall into 3 principal guilds: aerial hunting of alate ants, tree bark probing, and ground foraging on mainly non-alate ants.

Aerial predators are the nightjars, swifts, bee-eaters, *Eurystomus* rollers, and swallows. The rollers forage only at mass crepuscular swarms of ants and termites. Swifts and swallows feed at swarms, but also on dispersed flying ants and other small insects. Nightjars (crepuscular and nocturnal) and bee-eaters (diurnal) seem to feed mainly on ants and other insects that are dispersed and not swarming.

The bark-probing guild includes wood-hoopoes and 3 genera of strongly myrmecophagous woodpeckers. They forage by probing and gleaning mainly woody vegetation; they also probe ants' nests in the ground (*Picus*), and hop on the ground to glean it near the bases of trees (*Jynx*, several species of *Campethera*). Woodpeckers (Picinae), of course, provide the one avian example of gross anatomical adaptation to myrmecophagy, with their thick skin, sticky saliva, hyoid horns, and extraordinarily long, worm-like, protrusible, mobile and barb-tipped tongues.

Ground foragers include a fourth woodpecker genus, the exclusively myrmecophagous *Geocolaptes*, which feeds gregariously in large territories, using a sentry, progressing mainly by hopping. The bulbul *Phyllastrephus terrestris* is another ant-eater that forages in small groups on the ground, by hopping. Several *Tockus* hornbills search the ground by active (if rather clumsy) hopping-running. All other species in this guild are quite long-legged walkers or hoppers, like larks, pipits, robins, chats and thrushes. They may be soft-billed or hard-billed. Most ants being small, there appears to be a body-size constraint to myrmecophagy among their avian predators, with few being larger than francolins (500 g) or even than lapwings (250 g). Bustards and *Ceratogymna* hornbills, ground and arboreal foragers respectively, are exceptionally large; ants, some of which may be eaten adventitiously, do not feature to any significant extent in their diets.

Acknowledgements

I thank R. Gabor, S. M. Head and D. Roberts who have helped in various ways with this study, and I am particularly grateful to P. Alexander-Marrack for providing the *P. eurystomina* material.

References:
Alexander-Marrack, P. (in press). Notes on a breeding colony of the African River Martin *Pseudochelidon eurystomina* in Gabon. *Malimbus*.
Brosset, A. & Erard, C. 1986. *Les Oiseaux des Régions Forestières du Nord-Est du Gabon*. Vol. 1. Ecologie et comportement des espèces. Société Nationale de Protection de la Nature, Paris.
Brown, L. H., Urban, E. K. & Newman, K. (eds) 1982. *The Birds of Africa*, Vol. 1. Academic Press, London.
Chapin, J. P. 1953. The Birds of the Belgian Congo, Part 3. *Bull. Amer. Mus. Nat. Hist.* 75A: 1–738.
Cramp, S. (ed.) 1988. *The Birds of the Western Palearctic*, Vol. 5. Oxford University Press.
Earlé, R. A. 1985. Foraging behaviour and diet of the South African Cliff Swallow *Hirundo spilodera* (Aves: Hirundinidae). *Navors. Nas. Mus. Bloemfontein* 5(4): 53–66.
Earlé, R. A. & Louw, S. v.d. M. 1988. Diet of the anteating chat *Myrmecocichla formicivora* in relation to arthropod abundance. *S. Afr. J. Zool.* 23(3): 224–229.
Erard, C. 1981. Sur les migrations de *Pseudochelidon eurystomina* Hartlaub au Gabon. *Oiseau et R.F.O.* 51: 244–246.
Fry, C. H. 1984. *The Bee-eaters*. T. & A. D. Poyser, Calton, U.K.
Fry, C. H., Keith, S. & Urban, E. K. (eds) 1988. *The Birds of Africa*, Vol. 3. Academic Press, London.
Hölldobler, B. & Wilson, E. O. 1990. *The Ants*. Belknap Press of Harvard University Press, Cambridge, Mass.
Keith, S., Urban, E. K. & Fry, C. H. (eds) 1992. *The Birds of Africa*, Vol. 4. Academic Press, London.
Oatley, T. B. 1970. Observations on the food and feeding habits of some African robins (Aves: Turdinae). *Ann. Natal Mus.* 20(2): 293–327.
Oatley, T. B. 1992. Turdidae (in part), in Keith, S. *et al.* (eds) *The Birds of Africa*, Vol. 4. Academic Press, London.
Tarboton, W. 1976. Aspects of the biology of *Jynx ruficollis*. *Ostrich* 47: 99–112.
Thiollay, J. M. 1970. L'exploitation par les oiseaux des essaimages de fourmis et termites dans une zone de contact savane-forêt en Côte d'Ivoire. *Alauda* 38: 255–273.
Turner, A. & Rose, C. 1989. *A Handbook to the Swallows and Martins of the World*. Christopher Helm, Bromley, U.K.
Urban, E. K., Fry, C. H. & Keith, S. (eds) 1986. *The Birds of Africa* Vol. 2. Academic Press, London.

APPENDIX

Taxa in *The Birds of Africa* (Vols. 1–4) not implicated in ant-eating

STRUTHIONIFORMES, PROCELLARIIFORMES, SPHENISCIFORMES, GAVIIFORMES, PODICIPEDIFORMES, PELECANIFORMES, Ardeidae, Scopidae, Ciconiidae, Balaenicipitidae, *Plegadis, Bostrychia, Platalea*, PHOENICOPTERIFORMES, FALCONIFORMES, *Acryllium, Ptilopachus, Ortyxelos, Rougetius, Rallus, Porzana, Aenigmatolimnas, Amaurornis, Porphyrio, Gallinula, Fulica*, Gruidae, Heliornithidae, *Tetrax, Ardeotis, Otis*, Jacanidae, Rostratulidae, Dromadidae, Haematopodidae, Recurvirostridae, Burhinidae, *Pluvianus, Charadrius, Pluvialis*, Scolopacidae, Stercorariidae, *Rissa, Gelochelidon, Sterna, Anous*, Rynchopidae, Alcidae, *Treton, Turtur, Oena, Columba*, PSITTACIFORMES, MUSOPHAGIFORMES, *Oxylophus, Clamator, Pachycoccyx, Chrysococcyx, Ceuthmochares*, Tytonidae, *Otus, Jubula, Bubo, Scotopelia, Athene, Strix, Asio, Zoonavena, Urocolius*, Trogonidae, Alcedininae, Cerylinae, *Bucorvus, Gymnobucco, Prodotiscus, Melignomon, Lullula, Alauda, Eremophila, Phedina, Pseudhirundo, Tmetothylacus, Campephaga, Lobotos, Calyptocichla, Chlorocichla, Pyrrhurus*, Bombycillidae, Cinclidae, Troglodytidae, Prunellidae, *Cossyphicula, Modulatrix, Arcanator, Pinarornis, Cichladusa.*

Address: C. H. Fry, Department of Biology, College of Science, Sultan Qaboos University, Box 32486 Al Khod, Sultanate of Oman.

© British Ornithologists' Club 1992

Systematics and micro-evolution

Peter R. Grant

Received 24 January 1992

Introduction

Darwin's theory of evolution by natural selection is the central theory of modern biology. It has been greatly modified and extended, for example by the facts of genetics and the concept of genetic drift. Nevertheless current evolutionary theory is recognizably Darwinian. Contrast this with systematics, a field of biology to which evolutionary theory applies. Systematics, the study of relationships among organisms, has been more than modified, it has been truly transformed, and the transformation has occurred relatively recently. For the first three quarters of the past hundred years systematists established relationships among taxa by using phenotypic data to assess similarities. With the advent of electrophoresis in 1966 (Hubby & Lewontin 1966), and subsequent development of biochemical and molecular techniques like DNA-DNA hybridization, DNA fingerprinting, and gene amplification and sequencing, systematics has become increasingly grounded in genetics. The second element in the recent revolution has been the development of cladistic principles (and others) to be used in the reconstruction of phylogenies. An avian systematist of the 1890s, allowed a return visit in the 1990s, would be delighted to see that a classification of all 9672 bird species of the world has been accomplished (Sibley & Ahlquist 1990, Sibley & Monroe 1990), would be pleased to recognize familiar taxonomic categories like species, genera and orders, but would be bewildered by the way in which we assign particular birds to them.

Our returning Victorian would be similarly amazed at how the modern Elizabethan uses systematic information to gain an understanding of evolution. Having identified systematic relationships among taxa we would like to know the processes that gave rise to them, by what routes, why, where and how quickly. This is a field of inferential investigation of past evolutionary processes. It is pursued in various ways. The search for fossils is the obvious, but often limited, way. Mathematical modelling can help by showing what could have occurred and what could not have occurred, given plausible assumptions. Investigation is also popularly pursued by studies of contemporary processes; by the study of behaviour, ecology and micro-evolution of existing populations, which are the products of those past evolutionary processes.

In this article I will describe how a study of micro-evolution as a contemporary, observable, process has been used to throw light on evolution in the past.

Micro-evolution

Evolution is organic change, change that takes place from one generation to another in the genetic constitution of a population. Small changes accumulating over long periods of time give rise to large differences, such as those between 2 species in different but related genera or families. Micro-evolution refers to the small individual changes.

I make a distinction between the genetic changes taking place from one generation to the next, micro-evolution, and the evolutionary forces such as natural selection acting within a generation that produce an evolutionary effect. Natural selection occurs when some individuals in a population survive or reproduce better than others because they possess traits that enable them to perform better in that particular environment. If there is a heritable basis to those traits then the genes governing them will be passed on to the next generation. Differential gene transmission to the next generation is micro-evolution. Evolutionary processes other than natural selection may also give rise to or contribute to micro-evolution: sexual selection, mutation, immigration and drift.

I next make a distinction between selection inferred and selection observed.

Natural selection and adaptation

Differences between related taxa are in need of explanation. For example, birds on islands are often larger, and have larger beaks, than their relatives (same or different species) in nearby continental regions (Murphy 1938, Grant 1965). If islands have been colonized by birds from the mainland, as is likely to be generally the case, and evolution has been greater in the island population than in the mainland population since the time of colonization, the traits of the island birds need to be explained. Adaptation is suggested when the traits can be associated with some feature of the island, for example when beak size can be correlated with food size (Grant 1965, 1966, 1968, 1979a,b). The role of natural selection has been inferred.

The functional significance of variation in external traits like beak size is relatively easy to assess (Bowman 1961), and this facilitates investigation of adaptation (Arnold 1983). The task is much more difficult with internal anatomical features. Absence of association between trait expression and environmental characteristic suggests that evolution has proceeded by random processes like founder effects and drift. Models of the expected rate of divergence under drift can be employed to make quantitative tests of the drift (or selection) hypothesis (e.g. Baker *et al.* 1990).

Natural selection as a contemporary process

The direct study of natural selection requires something very different. It requires following the fates of known individuals through time to see if success or failure in survival and reproduction (fitness) is associated or not with the possession of a trait or the particular expression of a trait. An early example is the demonstration in 1974 of non-random survival in 2 populations of Darwin's Finches on the Galápagos island of Daphne Major. Surviving Medium Ground Finches *Geospiza fortis* had longer bill tips than non-survivors, and surviving Cactus Finches *G. scandens* varied less in weight and beak depth than non-survivors (Grant *et al.* 1976). The first is an example of directional selection, the second an example of stabilizing selection.

Since then there have been several studies of natural selection in bird populations, carried out mainly in the last dozen years and for different purposes. Price & Boag (1987) summarized the first ones, and discussed methods of analysis (see also Endler 1986). More recent studies have included selection on plumage variation (Møller 1989, Grant 1990, Hill 1991), on various morphological attributes including beak size and body size variation (Grant & Grant 1989a,b, Smith 1990, Hakkarainen & Korpimaki 1991, Witzell 1991) and on migratory tendency (Berthold 1991).

While quantitative, observational, studies such as these are needed to document, describe, and measure natural selection, they can do no more than suggest the causes of selection. Experiments are required to test selection hypotheses that specify causes.

Heritable variation

The direct study of micro-evolution requires that there be heritable variation. The methods of quantitative genetics have been applied to many of the same populations that have been investigated for evidence of natural selection. Boag & van Noordwijk (1987) provide a thorough review of methods, problems and accomplishments. A general finding has been that morphological traits such as beak size and body size have high heritabilities, whereas life history traits such as clutch size have lower but not negligible heritabilities. There is heritable variation in migratory tendency (Berthold 1991) and plumage traits (Møller 1989, Grant 1990, Hill 1991). Indeed the absence of significant heritable variation for well investigated traits (e.g. Gibbs 1988) is the exception rather than the rule, at least according to published studies.

DARWIN'S FINCHES

Micro-evolution of Darwin's Finches has been studied on Isla Daphne Major. The island is small (0.34 km^2), close to the equator in the centre of the Galápagos archipelago, and 8 km from the nearest large islands of Santa Cruz and Baltra. Two species have resident populations; *Geospiza fortis* (Medium Ground Finch) and *G. scandens* (Cactus Finch). Two others occasionally immigrate and rarely stay to breed: *G. fuliginosa* (Small Ground Finch) and *G. magnirostris* (Large Ground Finch). Birds have been ringed and measured since 1973. Breeding has been studied in every year when it has occurred between 1976 and 1991, almost all nests have been found, nestlings ringed and the parents identified by observation. Harmonic mean breeding population sizes were 197 *G. fortis*, 94 *G. scandens*, 6 *G. fuliginosa* and 4 *G. magnirostris* (Grant & Grant 1992).

Natural selection

Three episodes of natural selection have been witnessed (Table 1) at times of high mortality. The first and strongest occurred from late 1976 to the end of 1977. Almost no rain fell between March 1976 and January 1978. Of the 640 ringed *G. fortis* alive at the beginning of this period only 97 (15%) survived to the end. Mortality was size-selective; large birds survived better than small birds. *G. scandens* experienced a similar size-selective mortality, although less intensely. Survival was 42%.

TABLE I

Heritabilities and coefficients of selection for 4 morphological traits of *Geospiza fortis* on Isla Daphne Major. Selection coefficients are standardized selection differentials. Sample sizes refer to pairs of parents followed by numbers of offspring in the heritability column, and numbers of measured birds alive before selection occurred in the other columns. [1] = not significantly different from zero ($P > 0.05$).

	Heritability	Selection coefficients		
	h^2	1976–1977	1981–1982	1984–85
Weight	0.91	0.62	0.15	−0.18
Bill length	0.65	0.49	0.13	−0.09[1]
Bill depth	0.79	0.60	0.12	−0.18
Bill width	0.90	0.49	0.08[1]	−0.21
Sample sizes	39, 82	640	197	496
Mortality	—	0.85	0.35	0.64

Dry conditions occurred again in 1981–1982, and *G. fortis* was subjected to the same directional selection, though to a smaller degree than in 1977. Survival was much higher (65 %) this time.

The final episode occurred in the aftermath of an extremely severe El Niño event in 1982–83, which brought an extraordinary amount of rain to the Galápagos and resulted in some finches breeding for as many as 8 times. Breeding occurred twice in 1984, and then not again until 1987, another El Niño year, except for attempts made by some individuals in 1986. During the dry period without breeding from mid-1984 to the end of 1985 *G. fortis* were subjected to natural selection in the opposite direction; small birds survived better than large birds. From 1987 onwards mortality has been random with respect to size.

The targets of natural selection

When forces of selection act on one trait, other traits which are correlated with it are affected. Phenotypic correlations among the measured morphological traits are all positive and moderately large in the 3 populations of Darwin's Finches that have been studied in detail: *G. fortis* and *G. scandens* on Daphne (Boag 1983) and *G. conirostris* on I. Genovesa (Grant 1983). Thus when natural selection occurs, all traits shift in the same direction, although to different degrees, and it is not possible to determine by inspection of coefficients of overall selection like those in Table 1 whether selection acts on one or a suite of traits.

The problem of identifying the targets of selection is solved by using Lande & Arnold's (1983) multiple regression method which separates the direct association between fitness and a trait from the indirect ones, arising from correlations among traits (see also Crespi 1990). Price *et al.* (1984a) applied this method to the Daphne data from 1976–77 and found that the 4 traits listed in Table 1 were selected in different directions: weight and beak depth to increase and beak width to decrease. Beak length was not selected at all. Beak width was selected to decrease in 1984–85 as well (Gibbs & Grant 1987).

Identifying the targets helps in the interpretation of selection. Boag & Grant (1981) hypothesized that large birds survived the drought of 1977 relatively well in part because, possessing deep beaks, they were able to crack the large and hard seeds that remained in moderate abundance after the initially large stock of small seeds had been depleted. The analysis of targets supports the hypothesis, but reveals other targets not explained by it. Similarly Gibbs & Grant (1987) could account for selection in the opposite direction in terms of an altered composition of the food supply.

Heritable variation

Beak and body size traits display high levels of heritable variation. Boag (1983) regressed measurements of fully grown *G. fortis* offspring on mid-parent values to obtain the estimates shown in Table 1. All are significantly different from zero. Heritabilities of other measured traits, wing and tarsus length, are similarly high.

Micro-evolution

With such high heritabilities and strong coefficients of selection, evolution is expected to occur. The product of the heritability of a trait and the selection coefficient gives the simplest prediction of an evolutionary response to selection (Falconer 1989). More complicated formulations take into account the correlations among traits (Lande 1979, Price & Boag 1987). These will be discussed below. Boag (1983) used the first component from a principal components analysis of all morphological measurements to characterize overall body size, calculated the heritability of this synthetic trait (0.75) and the selection coefficient during the 1976–77 episode, and predicted an evolutionary response to selection of 0.40 standard deviations. The actual response in this trait—the difference between the population average before selection and the average in the next generation born in 1978—was 0.36 standard deviations, and hence close to the predicted amount. Therefore micro-evolution had occurred, as predicted: average body size was larger in the next generation as a result of a small scale evolutionary change.

Evolution occurred in the opposite direction in 1984–85. The generation born in 1987, like their parents, were smaller on average than the population in 1984 before selection had occurred.

The magnitude of selection and evolution can be most simply expressed as a percentage change in the mean of a population. For example, the selection episode of 1976–77 resulted in an increase in mean beak depth of about 5%. Evolutionary change was a little more than three quarters of this, c. 4%. Selection in the opposite direction in 1984–85 resulted in a shift in the mean of 2–3% and an evolutionary change in the same range.

Changes accompanying speciation

Clusters of Darwin's Finches differ from each other in size and shape, but not in plumage colour and pattern (Lack 1947, Grant 1986). The systematic relationships among them are not well established. Nevertheless biochemical similarities (Yang & Patton 1981) closely parallel morphological similarities (Schluter 1984), and agree in defining as one cluster the 6 species commonly known as ground finches (genus *Geospiza*). Within this group, what phenotypic and genetic changes took place during speciation and subsequently, and can modern studies of natural selection help us to understand these transformations?

First, comparisons of phenotypic data show the magnitude of the changes involved. Thus if ancestral *G. fortis* gave rise to *G. magnirostris*, without themselves undergoing any further change, then the difference between modern *G. fortis* and *G. magnirostris* represents the minimum change involved in speciation plus some fraction that occurred afterwards. These differences are relatively small. All coexisting species of ground finches differ in at least one beak dimension by at least 15% so another way of posing the same question is to ask how much selection is required to produce a shift of this size.

Secondly, genetic data show how much evolution can be expected from selection of a given magnitude. The heritabilities of all *G. fortis* traits are all high, so evolutionary changes should not fall far below those caused by selection. Heritabilities for *G. scandens* traits on Daphne are generally lower, and those for *G. conirostris* traits on Genovesa are intermediate (Grant 1983). Heritabilities for beak depth are 0.79 for *G. fortis* (Boag 1983), 0.80 for *G. scandens* (Price *et al*. 1984b) and 0.69 for *G. conirostris* (Grant 1983).

Thirdly, measurements of natural selection provide an estimate of how much change can be expected in single steps. The largest values obtained, in the study on Daphne are 5% for selection and 4% for evolution.

Putting these 3 quantities together yields the number of episodes of strongest observed selection that are sufficient to transform the beak depth of one species into that of another. The answer is 4. That is, 4 episodes of selection each resulting in an evolutionary change of 4% would result in a net change of 15%.

Speciation and multivariate evolution

Species are more than one dimension. The multidimensional equivalent to the preceding exercise requires an equation that incorporates several characters and their correlations. Lande's (1979) equation of multivariate evolution does this. A vector of phenotypic differences between 2 populations or species in several dimensions is equated to the product, as before, of heritability and selection; but now heritability is a matrix of genetic variances and covariances, and selection is a vector of the direct effects of selection on each of the characters independent of the correlated effects.

For the ground finches, the genetic matrix is known for one species, *G. fortis*, as are the several phenotypic differences between species, and they can be used to calculate minimal forces of selection in terms of a vector length. Vector lengths are found to be small when species differ principally in size, such as *G. fortis* compared with either *G. fuliginosa* (2.28) and *G. magnirostris* (2.76), and large when species differ in proportions, as is the case with *G. fortis* and *G. scandens* (15.39).

The vector length associated with the morphological changes in *G. fortis* brought about by the drought of 1977 was 0.12. Under selection regimes of this sort, approximately 20 such episodes would be required to transform *G. fortis* into *G. magnirostris*, a much larger number than was calculated by considering beak depth alone. Inclusion of other characters in the analysis is likely to increase that number. Nevertheless if one such episode occurred each century, the transformation of a population of *G. fortis* into *G. magnirostris* would take the comparatively short time of 2000 years. In contrast, the transformation from *G. fortis* to *G. scandens* would take about 13,000 years.

Conclusions

Measurements of the properties and performance of contemporary populations can be used to reconstruct past evolutionary processes. A knowledge of current selection regimes and heritable variation in Darwin's finch populations enables us to estimate the amount of selection that could account for differences between species. The principal results are that transitions between species differing largely in size could have proceeded rapidly, and more rapidly than for those differing in proportions owing to the constraining influence of genetic correlations between morphological traits. In reaching these conclusions I have ignored several complications (see Price *et al.* 1984b, Grant 1986, Boag & van Noordwijk 1987, Price & Boag 1987, Schluter 1989). These render questionable the accuracy of the calculations but not the overall result that selective forces are powerful enough to result in speciation relatively quickly. Sexual selection (Price 1984, Lande & Kirkpatrick 1988) and drift (Grant & Grant 1992) could have been contributing influences.

Discussion

The task of trying to understand the evolution of a particular group of organisms like passerine birds is made difficult by the incompleteness of the group. Many species, perhaps the vast majority, have become extinct, and it is unlikely that we will ever know much about them. Another difficulty arises from the fact that species may occupy geographical ranges far removed from their sites of origin. For example, British bird species probably did not evolve, as species, in Britain. Missing species and missing environments make evolutionary systematics a science that works with partial information.

Set against these difficulties are the successes which have been achieved in this and related disciplines. No class of organisms of comparable size is as well known systematically or biogeographically as birds. While animals like *Drosophila* are much better known genetically, the combined knowledge of ecology, behaviour, distribution, systematics and genetics of birds is without equal.

What can we expect in the future, and in particular from the study of micro-evolution? With the human genome project underway we can look forward to a time in the next century when some bird species will be completely characterized genetically. It is technically feasible to determine the complete architecture of avian genomes in individuals, and with this information to quantify precisely the variation among individuals within populations, between populations and between species; and it is feasible to determine the rates and sites at which new variants arise by mutation.

Expanding data banks of genetic information will permit advances to be made in 3 areas of relevance to this essay. First, they will permit refinements of systematic knowledge and the reconstruction of phylogeny. They will show in quantitative terms just how much genetic change is involved in speciation as well as in the evolution of higher taxa, and where in the genome those changes occur. Secondly, they will permit a deeper understanding of development, and of the interplay between the genome and its environment which occurs during development; in other words, a knowledge of genetic structure will facilitate the study of function. This information will be essential for understanding the genetic and developmental constraints on, and potentialities of, evolution (e.g. see Schluter 1989). The diversity of passerine birds has been produced by evolution subject to guiding rules which are scarcely understood. We do not know how malleable, genetically, species are, and in what ways.

Thirdly, they will deepen our knowledge of the genetic consequences of natural selection, and make more precise our understanding of the micro-evolutionary processes I have described in this paper. Eventually we may look forward to a detailed understanding of beak size and body size variation in genetic and environmental terms; to a knowledge of the number of genes involved, and to the sites, timing, mode and magnitude of their action. One of the reasons why micro-evolution of birds has not been studied more is the difficulty of capturing the adult offspring of known parents for heritability determination. Nevertheless there already exists an under-exploited potential to compare genetic characteristics of adults and young by molecular analysis of DNA extracted from blood samples from nestlings and parents. The potential will expand as genetic data banks expand, and intergenerational comparisons will be made in selected populations to determine the interplay of selection, drift and other evolutionary forces in bringing about evolutionary change.

Darwin's Finches have provided a good starting point for using micro-evolution to interpret larger evolutionary transformations that happened in the past. There is both need and opportunity to increase the scope of such studies. The traits investigated so far are entirely morphometric, which is appropriate because it is these that distinguish closely-related members of the ground finch group of species. But many species differ in plumage traits and only trivially if at all in morphometric traits. Plumage traits are important functionally as well as systematically. They may evolve under sexual selection and function in species recognition. Models of genetic variation and measurements of selection will provide the means of extrapolating from micro- to macro-evolution.

References:

Arnold, S. J. 1983. Morphology, performance and fitness. *Amer. Zoologist* 23: 347–361.

Baker, A. J., Dennison, M. D., Lynch A. & LeGrand, G. 1990. Genetic divergence in peripherally isolated populations of Chaffinches in the Atlantic Islands. *Evolution* 44: 981–999.

Berthold, P. 1991. Genetic control of migratory behaviour in birds. *Trends in Ecology and Evolution* 6: 254–257.

Boag, P. T. 1983. The heritability of external morphology in Darwin's Ground Finches (*Geospiza*) on Isla Daphne Major, Galápagos. *Evolution* 37: 877–894.

Boag, P. T. & Grant, P. R. 1981. Intense natural selection in a population of Darwin's Finches (Geospizinae) in the Galápagos. *Science* 214: 82–85.

Boag, P. T. & van Noordwijk, A. 1987. Quantitative genetics. *In* F. Cooke and P. A. Buckley (eds.) *Avian Genetics: A Population and Ecological Approach*, pp. 45–78. Academic Press, New York, N.Y.

Bowman, R. I. 1961. Morphological differentiation and adaptation in the Galápagos finches. *Univ. Calif. Publ. Zool.* 58: 1–302.

Crespi, B. J. 1990. Measuring the effect of natural selection on phenotypic interaction systems. *Amer. Naturalist* 135: 32–47.

Endler, J. A. 1986. *Natural Selection in the Wild.* Princeton University Press, Princeton, N.J.

Falconer, D. S. 1989. *Introduction to Quantitative Genetics.* 3rd edn. Longman, Harlow.

Gibbs, H. L. 1988. Heritability and selection on clutch size in Darwin's medium ground finches (*Geospiza fortis*). *Evolution* 42: 750–762.

Gibbs, H. L. & Grant, P. R. 1987. Oscillating selection in Darwin's Finches. *Nature* 327: 511–513.

Grant, B. R. 1990. The significance of subadult plumage in Darwin's Finches, *Geospiza fortis*. *Behavioural Ecology* 1: 161–170.

Grant, B. R. & Grant, P. R. 1989a. Natural selection in a population of Darwin's Finches. *Amer. Naturalist* 133: 377–393.

—, — 1989b. *Evolutionary Dynamics of a Natural Population: The Large Cactus Finch of The Galápagos.* University of Chicago Press, Chicago, IL.

Grant, P. R. 1965. The adaptive significance of some size trends in island birds. *Evolution* 19: 355–367.

— 1966. Ecological compatibility of bird species on islands. *Amer. Naturalist* 100: 451–462.

— 1968. Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. *Syst. Zool.* 17: 319–333.

— 1979a. Ecological and morphological variation of Canary Island Blue Tits, *Parus caeruleus* (Aves: Paridae). *Biol. Journ. Linn. Soc.* 11: 103–129.

— 1979b. Evolution of the chaffinch, *Fringilla coelebs*, on the Atlantic Islands. *Biol. Journ. Linn. Soc.* 11: 301–332.

— 1983. Inheritance of size and shape in a population of Darwin's Finches, *Geospiza conirostris*. *Proc. Roy. Soc. Lond.* B 220: 219–236.

— 1986. *Ecology and Evolution of Darwin's Finches.* Princeton University Press, Princeton, N.J.

Grant, P. R. & Grant, B. R. 1992. Demography and the genetically effective sizes of two populations of Darwin's Finches. *Ecology* 73: in press.

Grant, P. R., Grant, B. R., Smith, J. N. M., Abbott, I. & Abbott, L. K. 1976. Darwin's Finches: population variation and natural selection. *Proc. Nat. Acad. Sci. USA* 73: 257–261.

Hakkarainen, H. & Korpimaki, E. 1991. Reversed sexual size dimorphism in Tengmalm's owl: is small male size adaptive? *Oikos* 61: 337–346.

Hill, G. E. 1991. Plumage coloration as a sexually selected indicator of male quality. *Nature* 350: 337–339.

Hubby, J. L. & Lewontin, R. C. 1966. A molecular approach to the study of the genic heterozygoiety in natural populations, 1. The number of alleles at different loci in *Drosophila pseudoobscura*. *Genetics* 54: 577–594.

Lack, D. 1947. *Darwin's Finches.* Cambridge University Press, Cambridge, U.K.

Lande, R. 1979. Quantitative genetic analysis of multivariate evolution applied to brain: body size allometry. *Evolution* 33: 402–416.

Lande, R. & Arnold, S. J. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.

Lande, R. & Kirkpatrick, M. 1988. Ecological speciation by sexual selection. *Journ. Theoret. Biol.* 133: 85–98.

Lewontin, R. C. & Hubby, J. L. 1966. *Genetics* 54: 577–594.

Møller, A. P. 1989. Natural and sexual selection on a plumage signal of status and on morphology in House Sparrows, *Passer domesticus*. *Journ. of Evol. Biol.* 2: 125–140.

Murphy, R. C. 1938. The need for insular exploration as illustrated by birds. *Science* 88: 533–539.

Price, T. D. 1984. Sexual selection and body size, plumage and territory variables in a population of Darwin's Finches. *Evolution* 38: 327–341.

Price, T. D. & Boag, P. T. 1987. Selection in natural populations. *In* F. Cooke and P. A. Buckley (eds.), *Avian Genetics: A Population and Ecological Approach*, pp. 257–287. Academic Press, New York, N.Y.

Price, T. D., Grant, P. R., Gibbs, H. L. & Boag, P. T. 1984a. Recurrent patterns of natural selection in a population of Darwin's finches. *Nature* 309: 787–789.

Price, T. D., Grant P. R. & Boag, P. T. 1984b. Genetic changes in the morphological differentiation of Darwin's Ground Finches. *In* K. Wohrmann and V. Loeschcke (eds.), *Population Biology and Evolution,* pp. 49–66. Springer, Berlin.

Schluter, D. 1984. Morphological and phylogenetic relations among the Darwin's Finches. *Evolution* 38: 921–930.

— 1989. Bridging population and phylogenetic approaches to the evolution of complex traits. *In* D. B. Wake and G. Roth (eds.), *Complex Organismal Functions: Integration and Evolution in Vertebrates*, pp. 79–95. John Wiley and Sons.

Sibley, C. G. & Ahlquist, J. 1990. *Phylogeny and Classification of Birds: a study in molecular Evolution.* Yale University Press, New Haven, CT.

Sibley, C. G. & Monroe, B. L. Jr. 1990. *Distribution and Taxonomy of Birds of the World.* Yale University Press, New Haven, CT.

Smith, T. B. 1990. Natural selection on bill characters in the two bill morphs of the African Finch *Pyrenestes ostrinus*. *Evolution* 44: 832–842.

Witzell, H. 1991. Directional selection on morphology in the pheasant, *Phasianus colchicus*. *Oikos* 61: 394–400.

Yang, S.-Y. & Patton, J. L. 1981. Genic variability and differentiation in Galápagos finches. *Auk* 98: 230–242.

Address: Professor Peter R. Grant, Dept. of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544-1003, U.S.A.

© British Ornithologists' Club 1992

The history of species concepts and species limits in ornithology

Jürgen Haffer

Received 15 January 1992

CONTENTS

Introduction
Species concepts
  Morphological species concepts
  Biological species concept
  Historical 'species' concepts
Species limits
Ornithologists and species concepts
  Morphological species concepts
    Museum ornithologists: narrow species limits
    Explorer naturalists: wide species limits
      Old World: the Gloger–Middendorff school
      New World: the Bairdian school
    The pre-Darwinian species concept of Otto Kleinschmidt (1870–1954)
    Further developments
  The ascent of the biological species concept
  Population systematics
  Phyletic lineages as 'species'
  The changing number of species
Discussion
Acknowledgements
Summary
References

INTRODUCTION

At all times during the history of modern science, ornithologists contributed to the discussion of general biological concepts based on an exceptionally large amount of information that scientists and collectors had assembled from accessible and remote parts of the world. One such notion is the 'species', the basic unit in the systematic hierarchy of nature. The seemingly endless debate about the species problem over the last 200 years (Mayr 1957, 1982) has been fuelled and at times led by ornithologists. After a period of moderate stability around the middle of this century, the debate has gained momentum during the last 20 years. Therefore, a brief review of the history of the debate within ornithology would seem appropriate. I restrict my discussion to the period after ornithology had emerged as a separate scientific discipline during the first decades of the 19th century (Farber 1982), thus disregarding the important contributions of Ray, Linnaeus, Buffon, Kant, Cuvier and several other early scientists who laid the foundations of later work (Mayr 1982).

During the early stages of the debate, differences of opinion regarding the nature of species often reflected basic attitudes toward the concept of evolution. After the mutability of species in space and their transformation in time through the branching of phylogenetic lineages had been established beyond reasonable doubt, the debate about species shifted to another level. In current discussions, the term species refers to several quite different biological phenomena of evolutionary patterns and processes thereby leading to continuing arguments among the proponents of different concepts and preventing an agreement being reached.

In an introductory section, I present a brief overview of the various theoretical species concepts and of the different taxonomic species categories proposed. These topics have, of course, been the subject of a vast literature of which some titles will be mentioned below. In the main historical chapters, I follow several research trends in the development of species concepts among ornithologists and summarize several estimates of the changing numbers of bird species of the world.

SPECIES CONCEPTS

The species concept—the theoretical idea of the species—is a part of basic biological theory. During the early 19th century and before, the species concept was associated with theoretical ideas of typological essentialism and after Darwin, the species concept was part of evolutionary theory, e.g. the biological species concept as elaborated on by Mayr (1942, 1963). This species concept applies only to sexually reproducing organisms and it is truly valid only in nondimensional situations where species are sympatric or in parapatric contact. Historical 'species' concepts of cladists and palaeontologists refer to phyletic lineages rather than species.

The species as a theoretical notion (concept) needs to be distinguished from the species category within taxonomy to which actual species taxa are assigned (Mayr 1963). The taxonomic species category is, of course, based on the theoretical species concept, but it is a heuristic notion used to order the observed diversity in nature. The taxonomic species categories under different theoretical species concepts have been defined by different authors within narrow, intermediate and wide limits. The intermediate taxonomic species category under the theoretical biospecies concept is Mayr's (1963) multidimensional species category. The distinction between the theoretical species concept and the narrow to wide species category in taxonomy is reflected in the title of this article on species concepts and species limits. The much discussed 'species problem' refers to (1) the application of different theoretical species concepts and (2) the varying methods of delimiting species taxa, i.e. their assignment to differently delimited species categories in taxonomy. The main species concepts may be briefly characterized as follows (Mayr 1942, 1963, 1969):

MORPHOLOGICAL SPECIES CONCEPTS

Species are distinguished from other species and separated from subspecies (geographical 'varieties') on the basis of "degrees of morphological character differences" (rather than distinctness) and, in most cases, the fertility of conspecific individuals (rather than the isolation from nonconspecific populations). Ornithologists emphasizing the diversity of nature and applying a narrowly defined species category in taxonomy (i.e. circumscribing narrow species taxa) have been characterized as 'splitters'; others define the taxonomic species category more widely and emphasize the transitional nature of intergrading taxa and include wider arrays of geographically representative forms in more heterogeneous species taxa ('lumpers'). We may contrast a non-evolutionary (pre-Darwinian) and an evolutionary (post-Darwinian) concept of morphospecies. Species were assumed to possess certain constant features considered as "more essential" under the former view and "more primitive" under the latter viewpoint.

Non-evolutionary morphological concept. Under this theoretical species concept, the organic diversity reflects the expression of underlying 'types' and the observed variation is the result of different manifestations of the 'type'. This concept is typological, creationist and basically non-evolutionary.

Evolutionary morphological concept. Although the transformation of species and the branching evolution of organisms are accepted under this concept, species and subspecies are separated exclusively on the basis of morphological character differences and, in many cases, the fertility of conspecific individuals. Basically, this is the species concept of Charles Darwin in his *Origin of Species* (1859; not during the late 1830s) and of many zoologists during the late 19th into the 20th centuries.

This theoretical concept in a sense is transitional between the typological and biological species concept. W. Bock (pers. comm.) pointed out that, ultimately, it may not be possible to make a distinction between authors who accept an "evolutionary morphological species concept" and those who accept a "biological concept" but just use morphological differences to recognize different species taxa or make the distinction between what taxa are considered species and subspecies. Even today if one uses the biological species concept and the fundamental criterion of no genetic exchange between species, species taxa are recognized almost entirely on the basis of morphological differences between members of various species. Also individual organisms are identified as members of a particular species on the basis of morphological similarity. Although this is true, I feel there is a conspicuous difference between the theoretical views of authors who search for intrinsic, qualitatively different morphological characters of species (*versus* subspecies) and those who have the understanding that there is no intrinsic difference between the characters of species and subspecies and who just use morphological characters as indicators for geneflow actually or potentially to take place.

BIOLOGICAL SPECIES CONCEPT

"Species are groups of actually (or potentially) interbreeding natural populations that are reproductively isolated from other such groups" (Mayr 1942, 1963, 1969). Reproductive isolation is usually understood to mean genetic isolation, e.g. "possession of a shared genetic program is the common tie uniting individuals derived from the gene pool of a given species" (Mayr 1968: 164). Bock (1986) made this explicit by emending the definition to read "a species is a group of actually or potentially interbreeding populations of organisms which are genetically isolated in nature from other such groups". This emendation appears useful in view of the discovery in recent decades of several cases of representative taxa, especially of insects, that hybridize freely along the contact zone because of the lack of premating isolating mechanisms, but in which such cases hybrids are infertile because of fully developed postmating isolating mechanisms (parapatric hybridization). Some birds which meet along "zones of overlap and hybridization" (Short 1969) may also represent taxa which are genetically isolated but not reproductively isolated in a strict sense. These biological species would be considered as conspecific under Paterson's (1985) "recognition concept" of species. Panov (1989) and Grant & Grant (1992) reviewed the complex topic of hybridization and introgression in bird species as it relates to ethological isolation and the definition of the biological species border.

A fully differentiated biological species is a genetic unit, a reproductive unit and an ecological unit occupying a species-specific niche in nature (Mayr 1969, Bock 1986); it is capable of living sympatrically with other such species (synspecies—Sudhaus 1984). Taxa which replace each other geographically without or with only very restricted hybridization along the contact zone (paraspecies *sensu* Sudhaus 1984, as well as semispecies *sensu* Short 1969, respectively; see Table 1) are strong competitors owing to the lack of ecological isolation but have reached the level of biological species. It appears inadvisable to include ecological isolation in the taxonomic species definition (Mayr 1982: 273) since this would reduce semispecies and most paraspecies to the level of conspecific entities and would make the zoogeographical species (synspecies) the basic unit of the taxonomic system. Nevertheless, the process of microtaxonomic differentiation is not complete until genetic, reproductive, as well as ecologic isolation have been reached (Mayr 1942, Lack 1944, Bock 1979).

The biological species concept is nondimensional and can be applied readily (directly) only to sympatric or parapatric populations. It is the multidimensional species notion in taxonomy with its extensions over space and time which applies to most real units observed in nature, the species taxa, and which are subject to all the difficulties of any pragmatic application of theoretical concepts (Mayr 1963, 1982, Bock 1979, 1986). The distinctiveness of species becomes increasingly vague as one progresses geographically and chronologically further and further away from a single point where 2 species occur in sympatry or parapatry. The species category as a part of the taxonomic hierarchy should be defined broadly as the multidimensional species notion (many authors, however, applied fairly narrow limits to their taxonomic species category). Moreover, this category should be sufficiently broad and pragmatic to include species taxa of nonsexually reproducing organisms. We should also realize that it may well not be possible to formulate a single multidimensional species notion which is applicable to all known organisms.

On continents, intergradation of contiguous populations or their geographical exclusion without hybridization along the contact zone determines their rank as subspecies and paraspecies, respectively. Allopatric populations are assigned subspecies or species status on the basis of

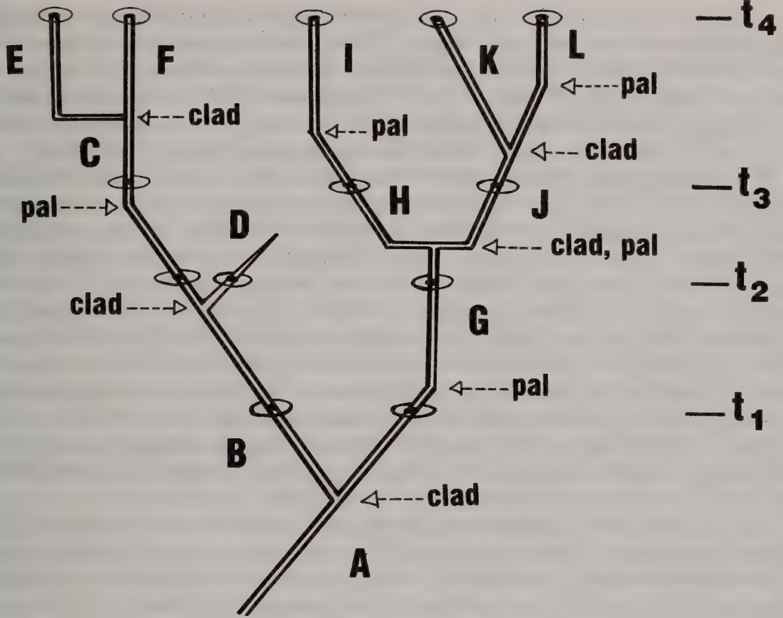


Figure 1. Several imaginary phylogenetic lineages to illustrate 'species' limits under the cladistic concept (clad.) and the palaeontological concept (pal.). Schematic representation. Groups of populations representing the various lineages at particular time levels (e.g. t_1–t_4) are different biological species (oval circles). Vertical scale—geological time; horizontal scale—morphological and other biological changes. A–L represent palaeontological 'species', except C–F, which together are one palaeontological 'species' but represent 2 cladistic 'species'.

inference (Mayr 1969: 197). For example, the Serin *Serinus serinus* and the Canary *Serinus canaria* were considered allopatric species because of their conspicuous differences in colour, shape of the bill and song which were interpreted as potential isolating factors. The Serin has invaded the Canary Islands in recent years, where it now lives sympatrically with *S. canaria* on several islands thus demonstrating its specific distinctiveness (which, of course, it had possessed already in allopatry, although unchallenged).

It may be advisable in the future to establish a scale for labelling species taxa by a number or a symbol according to the estimated reliability of their delimitation. Species taxa consisting exclusively of well differentiated allopatric subspecies or several monotypic species on islands would be low on this scale, whereas more widespread monotypic species on continents as well as polytypic species consisting of directly intergrading subspecies would be high on this 'reliability scale'.

The 'horizontal' concept of the biospecies (Fig. 1) refers to genetically isolated reproductive communities of a particular time level such as the Recent period or any other time level of the geological history of the earth (Peters 1970, Bock 1979, 1986). The vertical extent ('thickness') of such a geological time 'level' ('slice') or in other words the "duration" of a species is a matter of convention and, in most cases, will be determined by the incompleteness of the fossil record. The term 'chronospecies' has been used for artificially delimited and fairly extensive portions of phylogenetic species lineages (e.g. Remane 1985, Willmann 1985). Anagenetic change of a phylogenetic lineage through time does not signify 'speciation', which term refers here exclusively to the phenomenon of lineage splitting.

Morphologically differentiated taxa which merge through broad or narrow hybrid zones are combined as subspecies and megasubspecies of one biological species (Amadon & Short 1976 and in this volume). Admittedly, this procedure fairly frequently subsumes under one species name, and thus 'conceals' at that intermediate level, 2 or more conspicuously differentiated entities with independent biogeographical histories. A biogeographical species (Mayr & Short 1970, Bock & Farrand 1980, synspecies—Sudhaus 1984) comprises a superspecies or an independent biological species (which is not a member of a superspecies). Biogeographical species represent communities of descent and are the highest taxa which, on the basis of the genealogical relations and allo/parapatric distribution patterns of the component forms, can be delimited objectively (Rensch 1934: 51, Mayr 1942: 169).

The distribution patterns of groups of closely related parapatric biospecies resemble large scale mosaics composed of neatly interlocking patches formed by the ranges of the component species. Parapatric and allopatric biospecies are combined in a superspecies if they ". . . were once races of a single species but which now have achieved species status" (Amadon 1966, 1968). Geographically representative and closely related species are included in a superspecies even if their ranges overlap to a certain extent and the width of overlap is narrow relative to the vagility of taxa involved and the respective total ranges occupied (the amount of overlap is undefined). Component biospecies of superspecies have been designated paraspecies (Prigogine 1980, 1984a,b, Sudhaus 1984) if they are in contact, restricting the term allospecies (Amadon 1966) to geographically separated representatives. In some groups of animals parapatry probably persists long after the respective populations have attained genetic isolation and not only one but 2 or more speciation events have taken place (Haffer 1986).

Cladistically, the representatives of a superspecies are in most cases each others' closest relatives because of a basically consistent association between character evolution, genetic-reproductive isolation and ecological differentiation. However, detailed analyses may reveal that this is not true in some cases when one of the representatives of a superspecies is the sister taxon of another widely sympatric species. It remains to be determined how frequent such situations actually are. Selander (1971), Vuilleumier (1976) and Mayr (1980b) discussed various general aspects and problems of the application of the biological species concept to the avifaunas of the world.

The informal term 'species group' refers to a group of closely related species with extensively overlapping ranges (Mayr 1963; ex-superspecies —Vuilleumier 1985). These species have attained reproductive-genetic isolation from and ecological compatibility with each other; they are fully biologically compatible.

HISTORICAL "SPECIES" CONCEPTS

'Vertical' species concepts here combined under the designation 'historical' concepts or 'phylogenetic concepts' refer to portions of a phylogenetic lineage in time (Fig. 1). A 'vertical' lineage, however, represents an evolutionary phenomenon quite different from the notion of the 'horizontal' biological species discussed above (Bock 1979, 1986, Gittenberger 1972). A separate nomenclature and taxonomic system should be conceived to deal with phyletic lineages. The phyletic lineage is the continuum of a species as its members reproduce generation after generation through time. The phenotypic characteristics of the members of a phylogenetic lineage, and hence the underlying genetic bases, may remain the same over long geological periods (stasis) or change more or less gradually through time (phyletic evolution). A phyletic lineage may remain undivided over long periods or it may split (speciate) into 2 or more separate phyletic lineages from time to time (Bock 1986, Reif 1984). As Bock (1986: 38) and Szalay & Bock (1991: 15) have stated "A cross-section of a phyletic lineage at any point in time is a species (theoretical, non-dimensional). However, different time slices through the same phyletic lineage are not different species, nor are they the same species. They are simply different cross-sections of the lineage at different times, with the earlier one being ancestral to the later one. Each time slice is a species, but it makes no sense to ask whether they are the same or different species; the question lies outside the theoretical, nondimensional species concept and hence, from a theoretical perspective, is a non-question." In this sense a species has no origin, life span or age. The species populations of a phyletic lineage through time often altered their morphologies drastically at different time levels (phyletic evolution) and their biological relations to other contemporary species changed completely. No species boundary can be meaningfully placed along such a continuous lineage undergoing a rapid evolutionary shift or in the case of a branching lineage.

Of course, all phyletic lineages need to be studied in detail as they are important entities of the evolutionary history of a group of animals but, in contrast to species, they are not involved in the processes of evolution, i.e. phyletic evolution and speciation, which take place in living populations. Phyletic lineages "are the time paths (the record) resulting from the outcomes of these processes in species taxa. Phyletic lineages are history and as such are not involved in the ongoing process of evolutionary change; they do not have a role in the process itself. Species, not lineages, evolve and thereby have the proper claim to the attention of workers interested in the processes of evolutionary modification. Phyletic lineages have the proper claim for the attention of workers interested in analyzing the historical course of life" (Szalay & Bock 1991: 16). In their conclusion, these authors emphasize that "unless evolutionists and taxonomists make a clear distinction between these dual concepts (the species and the phyletic lineage), no hope exists to resolve the endless discussion on the ontology and epistemology of the species". The conceptual difference between the species of neontologists and the chrono-"species" of palaeontologists has been discussed by several other authors previously (e.g. Mayr 1942: 154, 1982: 292, Simpson 1961, Peters 1970, Bock 1979, Remane 1985).

The differences between the 2 historical "species" concepts refer to a different delimination of "species" as portions of phyletic lineages (Fig. 1). I designate Simpson's (1961) concept as "palaeontological" and the concept of Hennig (1950, 1966) as "cladistic". The designation 'evolutionary species' for the palaeontological concept is ambiguous, as this name has been applied also to certain cladistic concepts in recent years.

Palaeontological "species" concept. Palaeontologists, beginning with Simpson (1951, 1961), defined the species as follows: "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." Under this concept, species limits may or may not coincide with speciation events, i.e. branching of lineages.

Cladistic "species" concept. Hennig (1966: 59) considered a species as a phyletic lineage between 2 successive speciation (branching) events or until the lineage terminates (see also Willmann 1985). Character change may or may not occur in the 2 daughter species. Other definitions are "A species is a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind" (Eldredge & Cracraft 1980: 92) or "Species are simply the smallest detected samples of self-perpetuating organisms that have unique sets of characters" (Nelson & Platnick 1981: 12) and "A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (*"phylogenetic species"*—Cracraft 1983: 170). Cracraft and other cladists delimit "species" narrowly to be certain that these taxa are monophyletic, whereas Hennig (1966), Willmann (1983, 1985, 1986) and others apply the concept of monophyly only to groups of species. Accordingly, the latter authors delimit species more widely (as is done under the biospecies concept). Donoghue (1985) and Mishler & Brandon (1987) also proposed a "phylogenetic species concept" which, besides a grouping component (monophyly in the cladistic sense), recognizes a ranking component (e.g. interbreeding, selective constraints, or strong developmental canalization). This leads to narrow or broad delimitations of species taxa. According to most cladists, the life of an ancestral "species" ends when it splits into 2 new "species". Wiley (1981: 35), however, does permit the budding off of a "species" from another one which survives the speciation event. See further discussions of cladistic "species" concepts by Frost & Hillis (1990) and by several authors in *Cladistics* 5 (1989) and 6 (1990).

SPECIES LIMITS

Under each of the theoretical species concepts mentioned above, zoologists delimited and are delimiting 'narrow' or 'wide' species taxa depending on the placement of the species limit at 'low' or 'high' levels of microtaxonomic differentiation, respectively. In other words, based on each theoretical species concept, systematists devised differently conceived (wide to narrow) heuristic species categories in taxonomy used to order the observed diversity in nature. A species limit at a fairly high level of differentiation results in relatively few species taxa with each species comprising wide arrays of variously differentiated geographical representatives, whereas a species limit at a low level of differentiation results in more numerous, rather uniform, narrowly defined species taxa.

Following Mayr (1942, 1963), Lack (1944, 1971), Short (1969, 1972), Bock (1979, 1986) and others I have schematically subdivided the process of microtaxonomic differentation into 6 stages (Table 1). Each of the intermediate levels between one fairly uniform species (stage 1) and 2 fully biologically compatible synspecies (stage 6) are represented in the world's avifaunas by differentiated bird populations in contact. These stages are here listed in a presumed temporal sequence of gradually increasing microtaxonomic differentiation. Aspects of behavioural differentiation between closely related forms are subsumed under "genetic isolation" (e.g. differing types of song) and/or "ecological separation" (e.g. different feeding behaviour) and may be the cause of genetic or ecologic isolation between these relatives. Examples of such behavioural differences are many species of dabbling ducks whose reproductive isolation is maintained through different courtship behaviour and many species of North American warblers (Parulidae) and Holarctic tits (*Parus*) whose coexistence is maintained through different feeding behaviour and different feeding stations in trees.

Table 1 is an attempt at visualizing the process of microtaxonomic differentiation through a schematic grid of increasing levels of morphological, genetic-reproductive and ecological differentiation. The grid and, in particular, the sharp boundaries of the various stages (microtaxonomic categories) are rather crude means of schematically illustrating the results of the differentiation process. Nature is not necessarily orderly and extant faunas provide many examples of taxa at transitional stages between the categories distinguished here or of taxa which combine aspects of 2 categories in different areas of contact (e.g. hybridization occurring in one area of contact and overlap of their ranges to some extent without hybridization in another area of contact). Morphological differences may or may not render a group of populations diagnosable taxonomically at an early stage of differentiation (subspecies). In some bird populations genetic isolation may be completed before ecological segregation from the nearest relative is reached. This situation leads to geographic replacement (parapatry) of these forms when they come into contact (with no or only limited hybridization). The frequent occurrence of superspecies in the avifaunas of the world (Sibley & Monroe 1990) indicates that ecological competition often prevents sympatry of geographical representatives long after speciation is complete (Lack 1944, Mayr 1963). Many species probably perfected ecological segregation and certain aspects of reproductive isolation in neosympatry, but not genetic isolation, which must evolve fully in the initial allopatric period (Bock 1979, 1986, Grant 1986). The process of speciation has terminated only after the differentiating taxa have attained genetic-reproductive *and* ecological separation (leading to sympatry of synspecies). Under the biospecies concept, most authors currently place the limit of the taxonomic species category at level III (Table 1), as discussed by Short (1969,

TABLE 1

Components of microtaxonomic differentiation. Taxa at various stages of increased modification are assigned to collective taxonomic categories listed at right and here named under the biological species concept. Dashed lines indicate the position of the species limit under different taxonomic categories as follows: narrow cladistic 'species' category (I, II), multidimensional species category and broad cladistic 'species' category (III), species category under the recognition concept (IV), biogeographical species category (V)

Stages in the differentiation process		Relations between taxa along contact zone	TAXA Level of differentiation reached Morphological differentiation	Genetic isolation	Reproductive isolation	Ecological separation	Taxonomic categories	
6		SYMPATRY	(+)	(+)	(+)	(+)	Synspecies	
								V
5	PARAPATRY	COMPETITION PARAPATRY	(+)	(+)	(+)	–	Paraspecies	
								IV
4		HYBRIDIZATION PARAPATRY OVERLAP & HYBRIDIZATION PARAPATRIC HYBRIDIZATION	(+)	(+)	–	–	Semispecies	
								III
3	HYBRIDIZATION	NARROW HYBRID ZONE	(+)	–	–	–	Megasubspecies	
								II
2		WIDE HYBRID ZONE	(+)	–	–	–	Subspecies	
								I
1		CLINAL VARIATION	–	–	–	–		

(+), Present; –, absent.

1972). Hennig (1966) and Willmann (1985, 1986) also delimit the species category at approximately this intermediate level of differentiation, whereas other cladists (e.g. Nelson & Platnick 1981: 12, Cracraft 1983) delimit the taxonomic species category at the lower levels I or II.

Not all speciating taxa pass necessarily through all stages of the microtaxonomic differentiation process (Table 1). Small founder populations on islands, originating presumably from few individuals and speciating in bottleneck situations during peripatric speciation (Mayr 1982), probably differentiated rather quickly and directly from low to high levels of microtaxonomic modification (mode "Type Ib: speciation by the founder effect"—Bush 1975: 346). On the other hand, many continental species that differentiated through 'splitting' from fairly large isolated populations resulting from fragmentation of an ancestral species range ("Type Ia: speciation by subdivision"—Bush 1975: 341; dichopatric speciation—Cracraft 1984) probably originated more slowly through general genetic transformation (Mayr 1987: 312). Bush (1975: 341) referred to this mode of speciation as "a relatively long-term process". Consequently, taxa at various intermediate levels of microtaxonomic differentiation are comparatively common in continental faunas. The separation of populations leading to peripatric and dichopatric speciation had been designated, respectively, as primary and secondary disjunctions by Hofsten (1916). He showed that the occurrence of these 2 different types of discontinuities was already well-known to Forbes, Darwin, Wallace and other early biogeographers.

ORNITHOLOGISTS AND SPECIES CONCEPTS

During the past 200 years, ornithologists have used the different species concepts discussed above to classify the numerous kinds of birds of the world. Under each theoretical species concept, systematists delimited species taxa within wide, intermediate or narrow boundaries, i.e. they assigned species taxa to differently conceived species categories within taxonomy. From these considerations, I have constructed Table 2 listing the theoretical species concepts along the horizontal axis and subdividing each concept along the vertical axis according to wide, intermediate and narrow limits of the respective species categories in taxonomy. In this Table, I have placed a selective number of ornithologists at a position approximately corresponding to their theoretical viewpoints regarding the species as a theoretical concept (horizontal axis) and as a category within taxonomy (vertical axis). Additional ornithologists are mentioned in the text. Certain aspects of the taxonomic species category applied by a systematist can be deduced from his narrow to wide delimitation of species taxa. On the other hand, his theoretical species notion, i.e. his typological-creationist or evolutionary attitude, is often far less obvious and more difficult to ascertain. Therefore details of the taxonomic species categories applied by ornithologists are treated in more detail in the following pages than details of their underlying theoretical species concepts.

Schematic Table 2 and, in particular, the sharp distinction of the theoretical concepts do not permit an illustration of the numerous

TABLE 2

Theoretical species concepts (horizontal) and species limits under different taxonomic species categories (vertical) as applied by some ornithologists during the 19th and 20th centuries, supplemented by the names of several cladists and palaeontologists. Years refer to major publications; see text for details. Further literature search probably will reveal certain cladistic and palaeontological authors, who delimited species widely or narrowly, occupying the blank boxes of this table.

Species concepts / Species limits	1. MORPHOLOGICAL (Concept of “difference”)		2. BIOLOGICAL (“Horizontal” concept) The reproductive community	3. HISTORICAL (“Vertical” concepts) The phylogenetic lineage	
	non-evolutionary	evolutionary		cladistic	palaeontologic
Wide	Gloger 1833 Middendorff 1853 Kleinschmidt 1926	Geyr 1924 Meinertzhagen 1954 Eck 1985	Hellmayr 1920s Stresemann 1919–1927		
Intermediate	Schlegel 1844 Blasius 1862	Darwin 1850s Baird 1870s Coues 1870s Allen 1870s Ridgway 1870s Grinnell 1921	Darwin 1830s Seebohm 1880s Hartert 1903–1922 Stresemann 1928 ff. Rensch 1929, 1934 Mayr 1942, 1963 Lack 1944, 1947 Bock 1979, 1986	Hennig 1966 and followers, e.g. Willmann 1985	Simpson 1961 and other palaeontologists
Narrow	Temminck 1815 Vieillot 1816 C. L. Brehm 1823, 1831	Sharpe 1899–1909 P. L. Sclater 1880s Hartlaub 1877 Reichenow 1913	Stepanyan 1974, 1978	Cracraft 1983 McKitrick & Zink 1988	

relations and interconnections between and among the various viewpoints which have certainly existed at all times. In addition, certain authors have not always been consistent in their work, applying to comparable situations sometimes wide species limits and on other occasions intermediate species limits. Despite these difficulties, Table 2 does permit a valid distinction to be made between the basic theoretical views of such well-known authors as, e.g., Sclater, Allen, Kleinschmidt, and others.

Stresemann (1927, 1951, 1975), Rensch (1929b) and Mayr (1942, 1963, 1982) discussed many aspects of the development of ornithological systematics in their wide-ranging studies, in particular regarding the microtaxonomic levels with which I am concerned in this article. Additional historical data have been mentioned by Miller (1955) and Sibley (1955). My emphasis will be on some of those aspects not covered or only briefly discussed in these publications. Biographies of most ornithologists mentioned below have been published by Mullens & Swann (1917), Gebhardt (1964 ff.), Gillispie (1970 ff.) and Means & Mearns (1988).

I am here concerned with the discussion of the species problem by ornithologists. A more comprehensive treatment would need to take also into consideration the interesting contributions of certain botanists, entomologists and malacologists during the 19th century, some of which have been insufficiently appreciated in the recent literature.

MORPHOLOGICAL SPECIES CONCEPTS

Nearly all zoologists of the 19th century applied morphological species concepts. This was the time of intensive geographical and biological exploration of the world. The museum specialists studied numerous animal collections which professional collectors had assembled abroad; most of these systematists placed species taxa in a narrowly defined taxonomic category of morphospecies. Several explorer-naturalists personally made large collections of birds, mammals and insects in the field during extended expeditions. They were able to apply to the study of the collected material their extensive field experiences and arrived at widely circumscribed species taxa (broadly defined taxonomic species category). In addition, they analyzed various general aspects of geographical variation in animals.

Museum ornithologists: narrow species limits

The narrow Linnaean species of many 19th century ornithologists comprised one morphologically defined taxon (a subspecies or a monotypic species in current terminology), frequently described on the basis of only one or two specimens which represented the 'type' of the species (in the sense of the Platonic typological type). Intermediate specimens were dismissed as hybrids possessing no more significance than any abnormal animal. These were the species of many museum workers in Europe, e.g. C. J. Temminck, L. P. Vieillot, R. P. Lesson, C. L. Brehm, H. Lichtenstein, N. A. Vigors, W. MacGillivray, C. L. Bonaparte, W. Swainson, G. R. Gray and others, during the first half of the last century as well as of several leading systematic ornithologists during the late 19th into the early 20th centuries, e.g., J. Gould, J. Verreaux, G. Hartlaub,

P. L. Sclater, R. B. Sharpe, E. Oustalet, H. E. Dresser, J. Cabanis, T. Salvadori and A. Reichenow.

These ornithologists increased greatly our knowledge of the regional diversity of the avifaunas of the world but none of them seems to have seriously pondered the problem of distinguishing "real species from local varieties", i.e. distinguishing "between those characters which were impressed on a species at its creation, and those which may be reasonably attributed to external agents", a problem which Strickland (1845: 219) clearly posited in his well-known report on the state of ornithology. Geographical population differences had been mentioned in the literature since the time of Linnaeus, Buffon, Kant, Zimmermann, Esper, Pallas, and even earlier, during the 18th century (Mayr 1963, 1982, Zirnstein 1981).

Throughout most of his life, John Gould (1804–1881) considered any sample of birds that differed morphologically as a morphospecies. However, his work on Darwin's bird collection from South America and the Galapagos Archipelago proved decisive, because it permitted Darwin to appreciate the importance of the phenomenon of geographic representation, one of the reasons for his accepting the theory of geographic speciation in early 1837 (Sulloway 1982a); e.g. that closely related species of *Rhea* and of *Mimus* replace each other on the mainland of South America and that most of the Galapagos landbirds, including the several forms of *Mimus*, were new species which are clearly allied to related forms on the South American mainland. Another crucial insight at that time was Darwin's realization that one could call several populations on different islands in the Galapagos Archipelago either varieties or species (Mayr 1982: 409). Gould also concluded correctly that "the Galapagos finches were not, as Darwin had previously thought, members of widely different genera or even families, but rather one peculiar group of thirteen species" (Sulloway 1982b: 21). Gould placed them in one genus and 3 closely allied subgenera. In later years, Gould occasionally commented on geographical colour differences in birds of the same species, e.g. "the Tits of Central Europe being far brighter in colour than British specimens" and "the like difference exists between specimens of the same species inhabiting Van Diemen's Land and the continent of Australia" owing to the greater density and cloudiness of the atmosphere in islands, he thought (Gould 1855).

Among the ornithologists of the late 19th century mentioned above, Cabanis, Reichenow, Sclater, Sharpe and Gadow did not deny the existence of subspecies or certain climatic varieties in nature. Sharpe and Gadow listed some of them in the volumes of the *Catalogue of Birds in the British Museum* which they prepared, designating these forms as "subspecies, α, β, γ" etc. (Sharpe 1874, Gadow 1883, 1884). However, they and a few other authors in the 'Catalogue' series (e.g. Hargitt in vol. 18) assigned binomial names to these subspecies as C. L. Brehm (1823, 1831) had done decades earlier, as well as E. Blyth (1850) and T. C. Jerdon (1862). The latter 2 ornithologists recognized conspicuous geographic variation in many species during the course of their extensive comparative studies of Palaearctic and Indian birds, yet preferred in practice to give each race a distinct specific name. Edward Blyth had corresponded with

Darwin during the 1850s. His discussion of the common descent of certain bird 'species', however, refers to geographical subspecies (which Blyth named binomially) and therefore does not mean that he implied transmutation of biological species. Jerdon (1862: xxxiii) pronounced: "That the species were created at hap-hazard, without any reference to others, either of the same group, or more distant ones, is a doctrine so opposed to all affinities and analogies observed throughout the animal world, that the mind refuses to accept it, and intuitively acknowledges the evidence of design". The use of the term "affinity" by Jerdon is in the sense of Strickland and is synonymous with "homology", but not in the sense of affinity as we would use this term today.

Many other museum ornithologists of the late 19th century very probably had accepted the theory of evolution, although this is not reflected in their taxonomic treatment of species and they never published their views on this or any related topic except, e.g., Reichenow (1893), Sclater (1896: 314) and also Alfred Newton, the doyen of British ornithologists at that time. He had been one of the first biologists to adopt the Darwinian theory of natural selection on the basis of the Darwin-Wallace articles presented to the Linnaean Society on 1 July and published on 20 August 1858 (Gage & Stearn 1988). Newton immediately applied natural selection to the interpretation of a phenomenon in nature, i.e. the origin of desert coloration in several species of larks and chats of northern Africa, and discussed his interpretation in a long letter written on 24 August 1858 to H. B. Tristram, who directly accepted this view. He presented it, with only a general reference to Newton, in an article which appeared in 1859 several months prior to the publication of Darwin's 'Origin' (Tristram 1859: 429–433, Cohen 1985: 590). Thus Tristram (and not Newton) became "the one naturalist publicly to accept and to apply the new concept of natural selection before the publication of the Origin" (Cohen 1985: 592; see also Newton 1896: 79 and Burkhardt 1982: 42). Most ornithologists at that time and into the 20th century preferred a Lamarckian interpretation of such phenomena. On the other hand, Newton never gave a clear definition of what he thought a 'species' was, although it is obvious from the context of several discussions that he followed a morphological species notion. He did not include entries for 'species' or 'subspecies' in his well-known "A Dictionary of Birds" (1896), stating in the introduction (p. viii) "Nomenclature . . . owing to its contentious nature I have studied to avoid." Newton (1896: 343) agreed with the North American ornithologists' abolition of a great number of what had hitherto passed as distinct 'species', and their recognition as local forms, any 2 or more of which should be united under one heading. During his later years, P. L. Sclater (1896: 314–315) shared a similar opinion "on the vexed subjects of trinomials" stating that subspecies should be designated with a third name following the principles of the North American students of geographical variation of birds and mammals. As examples he listed the trinomial names of several British and continental forms of tits.

Many ornithologists of the late 19th century followed A. R. Wallace's (1858) advice: "You must consider every group of individuals presenting permanent characters, however slight, to constitute a species". In discussing the question "What is a species?", David O. Hume (1875) in India similarly concluded that species differ in essential (i.e. constant) characters, however small, and not bridged over by intermediate links. Under this concept, all morphologically differentiated allopatric varieties, e.g. those inhabiting islands, were raised to the rank of separate species.

Among North American zoologists applying a narrow morphospecies concept towards the end of the last century, was C. H. Merriam (1897: 755): ". . . forms which differ only slightly should rank as subspecies even if known not to intergrade, while forms which differ in definite, constant and easily recognized characters should rank as species even if known to intergrade". He described no less than 78 "species" of North American bears (see Hall 1981, vol. 2: 952–958) and numerous "species" of prairie wolves (coyotes). This led to an interesting discussion on the species question in *Science* (n.s. 5, 1897), initiated by no other person than Theodore Roosevelt, who disagreed from a field naturalist's point of view with Merriam's taxonomic "oversplitting".

Explorer-naturalists: wide species limits

Ornithological exploration of the vast and ecologically diverse continents of Eurasia and North America during the 18th and 19th centuries led to the discovery of numerous conspicuously different, but intergrading geographical forms of birds and mammals which the explorer-naturalists combined in rather broadly circumscribed species taxa. The European explorers were most active during the first half of the 19th century, their principal reports appearing in 1811, 1833, and 1840–1867. Most of them worked under the influence of the typological theories of natural philosophy, whereas in North America systematic ornithological exploration began somewhat later reaching a peak during the 1870s and 1880s after the publication of Charles Darwin's theories of evolution. The European explorer-naturalists studied their collections of birds and mammals at different museums and some of them became museum specialists. Most of the North American naturalists mentioned below were associated with the Smithsonian Institution in Washington or with the American Museum of Natural History in New York.

Old World: the Gloger-Middendorff school.

The founder of this research tradition was P. S. Pallas, who travelled in Siberia and the Far East (1768-1774). He was followed by F. Faber (Iceland 1819–1821), J. H. Blasius (Carpathian Mountains 1835, Russia 1840–1841), A. von Nordmann (southern Russia 1837), A. Th. von Middendorff (Lapland 1840, Siberia and Far East 1842–1845), L. von Schrenck (Far East 1854–1856), and G. Radde (eastern Siberia 1855–1859, southern Russia 1860s–1890s). Several of these men travelled under the auspices of the Academy of Sciences in Petersburg to explore territories of the vast Russian empire. Other early explorer-naturalists in the services of the Academy of Sciences in Petersburg who had travelled in eastern Europe and Asia during the 18th century were D. G. Messerschmidt, G. Steller, S. G. Gmelin, and J. A. Güldenstädt. The results of the researches of these latter workers have been utilized and in part published by P. S. Pallas. Constantin Gloger (1833, 1834, 1856a,b) and Hermann Schlegel (1844a,b), museum workers in Berlin and Leiden respectively, and naturalist travellers in Europe became influential among the above group of explorer-naturalists through their theoretical reflections on the nature of species and their discussions of general aspects of individual and geographic variation.

Peter Simon Pallas laid the foundations of zoological, geological, and geographical knowledge of vast portions of the Eurasian continent. He distinguished in his important 'Zoographia Rosso-Asiatica' (1811) between individual and geographical variation and found that numerous wideranging species consist of a mosaic of morphologically characterized climatic varieties (Stresemann 1962). His statement "Varietates nullas neglexi, quae in Zoologia maximi momenti certae sunt" influenced the work of those who succeeded him in the faunal exploration of Eurasia and led to their preliminary studies of the significance and cause of geographical variation. However, based on the strongly typological view of nature which soon developed under the influence of German idealism and Naturphilosophie, Gloger, Schlegel and Blasius (as nearly all other European naturalists at that time) conceived species as immutable natural entities which had independent origins and varied geographically within definite limits (due to climatic or other environmental influences). Schlegel in Leiden (Netherlands) eventually became convinced, like C. L. Brehm and the entomologist H. Schaum in Germany, as well as L. Agassiz in North America, that also all geographical varieties had existed since the beginning of creation and were immutable (Stresemann 1975: 200).

In his study of the birds of the far northern regions, Faber (1825) developed the view, confirming Pallas's, that many widespread species have changed their appearance due to the influence of the local environment (climatic races). C. L. Gloger's (1833: x) species definition was "What under natural conditions regularly pairs, always belongs to one species." He prepared the first comprehensive treatment of general aspects of the "Variation of birds under climatic influence" (1833), in particular with regard to plumage colour. This small book (159 pages) was originally prepared as the Introduction to Gloger's (1834) "Handbook" of the natural history of European birds when Gloger was in his twenties and still a student of natural sciences in Berlin (where he used the extensive bird collections) under H. C. Lichtenstein. The text was issued separately to come to the attention of a wider circle of naturalists outside the narrow field of ornithology. Stimulated by the observations of P. S. Pallas (the "excellent, well informed, true naturalist"), Gloger emphasized the regional intergradation of climatic varieties of birds which should not be separated artificially as "species". His theoretical species concept was typological and his taxonomic species category widely delimited. Gloger's observations on continuous gentle character gradients "which connect even the most distant extremes", anticipate the phenomenon of clinal character variation in current terminology. He also mentioned geographic variation of northwardly increasing body size, geographical differences of egg coloration, calls and song and even of behaviour and habitat preferences. Gloger (1833: 106–107) thought, however, that the character variation of geographical races is caused by direct influences of the climate and that the offspring of individuals of one variety, if transferred to the range of another one, would change to that plumage colour within a few years. He therefore proposed that climatic varieties not be named and existing names be placed under the synonymy of the species name, a suggestion which practically no later naturalist has followed.

Gloger (1833, 1834) concluded on the basis of intergradation as demonstrated by intermediate specimens that, e.g., *Sitta caesia* is conspecific with *S. europaea, Corvus cornix* with *C. corone, Motacilla lugens* and *M. lugubris* with *M. alba, Garrulus bispecularis* with *G. glandarius*. Many of Gloger's species coincide with current polytypic biospecies. In certain other cases, however, Gloger's 'lumping' tendency led him to combine as 'varieties' the vicariant members of species pairs, since he had no information on their relationship along the contact zones: *Hippolais icterina/ H. polyglotta, Emberiza caesia/E. hortulana, Sturnus unicolor/S. vulgaris, Phoenicurus erythrogaster/P. phoenicurus* and *Parus monticolus/P. major*. In the words of a leading contemporary ornithologist, Gloger's accomplishments "have been epoch-making and, even though questioned in part by recent research, and partly recognized as erroneous, have been highly stimulating in his time" (Hartlaub 1865: 1). Gloger's pioneering contributions were little appreciated during the late 19th and early 20th centuries until Rensch (1929b) and Mayr (1942, 1982) made reference to his work repeatedly.

The taxonomic philosophies of Pallas, Gloger and Schlegel were followed by the naturalists-explorers in their ornithological expedition reports: Nordmann (1840), Blasius (1844), Middendorff (1853, 1867, 1874), Schrenck (1859, 1860) and Radde (1862, 1863, 1884), all of whom compared their material with samples from western and eastern Europe. Only Nordmann, however, accepted Gloger's suggestion not to differentiate the geographical varieties by name. The other explorer-naturalists beginning with Middendorff followed Schlegel (1844a,b, 1854–58), who had, as the first zoologist, consistently applied trinomial nomenclature to a fairly large number of geographical varieties (his "conspecies"), the name of the conspecies following the species name directly, e. g. *Falco tinnunculus japonicus*. When he worked on the material which Ph. F. Siebold had collected in Japan, Schlegel (1844b) simply added the geographically descriptive term *japonicus* to the species name to characterize the morphologically deviating Japanese island population. He followed the same method (1844a) listing 22 geographical conspecies of European birds. Middendorff, Blasius and the other naturalists, however, inserted the expression 'var.' (*varietas*) between the species and subspecies name, as Sundevall (1840) had done in several cases before.

The ornithologists of the Gloger-Middendorff school used the term variety mostly, if not exclusively, in the sense of geographical subspecies. Other contemporary workers did not always distinguish individual from geographical varieties. Therefore, the use of the term variety was eventually abandoned (Mayr 1963, 1982).

Middendorff (1853) and the other naturalists had at their disposal many series of specimen samples representing numerous taxa from far distant regions of Eurasia. This material demonstrated various aspects of individual and geographic variation including the direct intergradation of many contiguous taxa of birds and mammals (bears, foxes, wolves, hares) in colour, measurements and form, thus revealing the conspecific nature of numerous narrowly conceived morphospecies of previous authors, e.g. the conspicuously different subspecies of such wide-ranging bird species as *Garrulus glandarius, Motacilla alba, Pyrrhula pyrrhula, Sturnus vulgaris* and *Eremophila alpestris*. Turning against one of his ornithological critics, Middendorff (1874: 1230) stated: "Nature appears very different to the travelling naturalist when he daily pursues his researches amidst the richest animal life, impressed by its endless shapes; and very different to the specialist handling a few dry skins in a museum." In a chapter entitled "Umfang des Artbegriffes" [Extent of the species notion], Middendorff (1867: 790–798) stated his basic agreement with Gloger's broad taxonomic species category but emphasized that he doubted in many cases the external cause of geographic variation to lie in climatic influences. He dismissed Darwin's transmutation theory because by far the majority of the (broadly delimited) species appeared to him sharply separated by bridgeless gaps. He favoured a typological species notion and stated that transmutation may apply to only few species taxa.

Nordmann (1840), Schrenck (1860) and Radde (1863, 1884) discussed similar taxonomic observations on the species which they had collected during their expeditions, so that several contemporary reviewers of their expedition reports spoke of the "Gloger school" (Homeyer 1868) or the "Middendorff school" (Hensel 1861). It is obvious from the publications of the members of these 'schools' that they considered themselves to be part of a research tradition. They referred frequently to the general discussions of Gloger and Middendorff. Radde (1884: 11) quoted the concepts of P. S. Pallas as the theoretical basis of his work. These explorer-naturalists realized at the same time that most contemporary ornithologists in Europe opposed their application of wide species limits (i.e. their broadly defined taxonomic species category). There were only few other taxonomists in Europe who followed Schlegel (1844a) in using, at least in some cases, trinomials for subspecies; e.g. Zander (1851) considered the various conspicuously different geographical forms of *Motacilla alba* and *M. flava* as conspecific and Wied (1858: 27, 101) listed trinomial names for 2 North American birds (*Otus brachyotus americanus* and *Hirundo riparia americana*).

Besides many taxonomic aspects of their collections, the ornithologists of the Gloger-Middendorff school also studied numerous general phenomena of geographical character variation of birds and mammals across Eurasia, especially the variation of body size and of the colour of plumage and pelage, respectively. In a lengthy chapter on 'The variation of Siberian animals', Middendorff (1867: 798–822) continued the tradition of Gloger (1833) and treated continental variation of vertebrates comprehensively emphasizing that body size of members of the same animal species increases from Africa through Europe to northeastern Asia (without, however, referring to Bergmann's earlier publication on this topic; regarding the history of Bergmann's Rule see Coleman 1979). Middendorff pointed out that a colourful and shiny plumage characterizes tropical birds, but not exclusively, as shown by the shiny portions of the plumage in such northern birds as *Luscinia suecica, L. calliope* and

Somateria spectabilis. He further stated that, under the cold continental climate of northeastern Siberia, plumage colour turns increasingly whitish in many bird species and, on the other hand, becomes gradually more intensive and darker under the humid oceanic climate of the coastal lowlands both east and west of the Bering Sea, extending into humid Amurland, where Schrenck (1860) had made similar observations. The latter explorer had stressed the fact that plumage colour in birds of the Amur region darkens through an increase in the black, grey, blackish brown and grey-brown pigmentation, with or without an extension of the dark portions of the plumage patterns.

The naturalists of the Middendorff school were too weak as a research group to constitute strong opposition to the leading, systematic ornithologists of their times (who applied narrow taxonomic species categories). The members of the Gloger-Middendorff school remained 'outsiders' during the 19th century. Moreover, since they published the results of their ornithological studies only in costly expedition reports which had limited distributions, their consistent emphasis on broadly defined species entities of Eurasian birds and mammals, together with their impressive data base on geographical variation, had not the impact among fellow workers of the scientific community as would have been desirable. Probably for the same reason, the research tradition of the Gloger-Middendorff school existing during the course of over 100 years (1770s to 1880s and beyond) has not been widely appreciated previously by ornithological historians, although the significance of the early work of P. S. Pallas has always been stressed.

Hermann Schlegel at Leiden and J. H. Blasius at Brunswick made great efforts to assemble, from the 1850s to the 1870s, series of specimens representing young and adult birds of the various geographical 'conspecies' in order to determine the range of individual and geographical variation of a species and to analyse regional trends in the variation of plumage colour and body size (Baldamus 1861, F. Schlegel 1867). They adhered to a similar typological species concept as Gloger (1833) and Middendorff (1853) but assigned species taxa to a somewhat less broadly defined taxonomic species category. In their lists of the birds of Europe, both Blasius (1862) and Dubois (1871) used subspecies names routinely, as Schlegel (1844a,b) had done. However, Blasius and Dubois designated the subspecies of a species with the letters α, β, γ, etc. They did not go as far as Gloger (and later Kleinschmidt) in 'lumping' certain geographical representatives into the same species; thus they circumscribed species at an intermediate level of microtaxonomic differentiation (Table 2). The list by Blasius (1862) was "privately printed" in Germany and an English translation issued by A. Newton. The catalogue by Dubois resembles that of Blasius but follows a different sequence. Both publications are scarce and little known. Dubois (1873) later discussed geographical variation in many birds, adding several subspecies to his previous list and deploring the application of narrow species limits by many leading systematists in Europe.

J. H. Blasius was not an evolutionist. He stated that a bridgeless gap separates 2 different species, "a sharply defined boundary, free from all gradual transitions must occur". If the characters of geographical forms intergrade, specific separation is not justified. Environmental factors may cause certain geographical deviations from the type; they cannot, however, destroy the integrity of the species. All species represent independent creations. An unshakeable order rules organic nature, as it also rules the worlds of crystals and stars (Blasius 1857: v, 1858, 1861). Most leading ornithologists in Germany at that time supported this typological and creationist, non-evolutionary viewpoint.

Only a few ornithologists had adopted Darwinian interpretations (e.g. F. Kutter, G. Jaeger, W. von Reichenau; see Stresemann 1975). Among the latter were also Anton Reichenow in Berlin and Hans Baron (later Count) von Berlepsch in Hannoversch-Münden. Reichenow had travelled in Central Africa during 1872/73. According to his Darwinian view "all extant animal species basically are varieties of older extinct forms" and the study of geographical variation was furnishing with inestimable material those naturalists who based their systematic studies upon the theory of evolution. At that time, Reichenow subordinated the geographical subspecies under the species category and delimited fairly wide species taxa, describing numerous geographical forms from Africa (Reichenow 1877, 1880). Since the early 1880s, Berlepsch applied trinomial nomenclature in his studies of neotropical birds, probably influenced by the practice of Coues, Allen, Ridgway and other North American ornithologists some of whom also worked on Neotropical birds. Berlepsch distinguished 16, 17 and 19 trinomially named subspecies among 216, 177 and 289 forms, respectively, in 3 separate publications on birds from western South America (e.g. Berlepsch & Taczanowski 1883). Stimulated by the discussion of trinomial nomenclature at the British Museum during the visit of E. Coues in 1884 (Sharpe 1884, see below) and at the suggestion of G. Hartlaub, the German Ornithological Society, during the same year, discussed and agreed on the modest use of subspecies names. Based on this official licence, several European ornithologists continued or began to apply trinomial subspecies names to a modest degree (besides Reichenow, Berlepsch, Taczanowski and Seebolm, also several Russian workers like Sewerzow, Bogdanow and Menzbier). L. Taczanowski in Warsaw had listed mostly narrow morphospecies in his work on Southern American birds during the 1880s but, in his summarizing treatment of the bird fauna of eastern Siberia, he discussed numerous trinomially named subspecies (Taczanowski 1891–1893). Berlepsch was an evolutionist (like Reichenow) and, during the early 1890s, he lectured on the genealogical relationships of certain groups of birds and on various aspects of Darwin's theory of natural selection. (Regarding Berlepsch's and Reichenow's later opinions on a peculiar use of trinomial nomenclature, see below.)

The contrasting views of most museum ornithologists in Europe and of the explorer-naturalists of the Middendorff group regarding narrowly and broadly defined taxonomic species categories, respectively, led to numerous controversies, particularly in Germany. Between 1826 and 1832 (in Oken's *Isis*), Faber, Gloger and Bruch repeatedly attacked C. L. Brehm's concept of a narrow taxonomic species category and his use of 'subspecies' discussing various aspects of individual as against geographical variation which Brehm had not clearly separated. This controversy lingered on in the literature until the German Ornithological Society (DOG) devoted its annual meeting in 1856 to an extensive discussion of the question "What is a species?" without solving the problem or reaching an agreement on the circumscription of species taxa. Temporary arguments flared up again after Darwin's publication of the 'Origin' (Stresemann 1975), but the museum specialists' view on a narrowly defined morphospecies category continued to dominate systematic ornithology in Europe and the work of the Gloger-Middendorff school fell into oblivion (hastened by an extensive unfriendly discussion of the ornithological work of Middendorff, Schrenck and Radde by a museum worker from the point of view of the narrow morphospecies concept—Homeyer 1868–1870). As mentioned above, few Old World ornithologists used subspecies names during the 1870s and 1880s until the turn of the century when, at the annual DOG meeting at Dresden in 1897, Hartert, Kleinschmidt, Berlepsch, A. B. Meyer and Wiglesworth again discussed the problem of subspecies and species, this time inspired by the work of the North American ornithologists.

New World: the Bairdian school

During the 1860s and 1870s, the leading ornithologists in North America, S. F. Baird, E. Coues, J. A. Allen and R. Ridgway, further developed the subspecies concept, after J. Cassin and S. F. Baird had named several geographical varieties of a number of species during the 1850s (Stresemann 1975, Mayr 1982, Sterling 1988). These workers began to apply trinomial nomenclature to a modest degree when Baird, Cassin & Lawrence (1860) listed some 'varieties' of *Picus villosus, Mniotilta varia, Tringa alpina* and *Bubo virginianus*, those of the latter species even without the usual expression 'var.' in front of the subspecific name. Their use of trinomial names increased conspicuously during the 1870s (Coues 1872, 1874, Baird, Brewer & Ridgway 1874) and during the 1880s, e.g. Ridgway (1881), who left off the expression 'var.' in front of the subspecies name routinely (as had Schlegel 1844a,b in Leiden) and Baird, Brewer & Ridgway (1884). In 1885, certain rules on the use of subspecies names were adopted unanimously by the American Ornithologists' Union and the slogan "Intergradation is the touchstone of trinomialism" (Stejneger 1884) became the guiding principle in North America (A.O.U. Code 1886, review by Allen 1890, 1908). Cutright & Brodhead (1981) summarized these developments, emphasizing the role of Elliott Coues, who was probably most responsible for the spread of trinomial nomenclature in North America.

In contrast to the typological and non-evolutionary (pre-Darwinian) concepts of most European workers, the theoretical views of this new generation of North American ornithologists were fully in accord with the theory of evolution (though regarding the mechanism of evolutionary change they preferred a Lamarckian interpretation—Allen 1871, Elliot 1892). Thus Coues (in Baird *et al.* 1874: 559), in a somewhat oversimplified manner, defined the geographical variety as "a nascent species". The North American ornithologists defined species morphologically like Wallace (1858), Hume (1875) and others had done (see above) stating that "a small amount of difference, if constant, was considered 'specific', in a proper sense, while a large amount of difference, if found to lessen and disappear when specimens from contiguous faunal areas were compared, was considered as not specific" (A.O.U. Code 1886, cited from Allen 1908: 594). Many allopatric forms were raised to the rank of separate species, whereas others were considered as conspecific based on overlapping individual variation or simply on personal judgment (Ridgway 1901: x).

The American ornithologists were working under the direction of S. F. Baird of the Smithsonian Institution (Washington), the leading vertebrate zoologist of mid-19th century America and a very able scientific administrator. Coues (1903) later designated this period the 'Bairdian Epoch' of North American ornithology.

The ornithologists of the Bairdian school had arrived at the grouping of intergrading subspecies into widely circumscribed species taxa through their analyses of extensive specimen material (series of adult and young birds of the same species from many different locations of a species' range), which they had collected as physicians and naturalists of several transcontinental military expeditions organized by the Geological Survey in Washington to explore locations for railroad routes in western North America. These expeditions were run in an east-west direction at intervals northwards between the Mexican and Canadian borders and the collections sent to the National Museum at the Smithsonian Institution. The analyses of these collections resulted in important contributions to the study and interpretation of individual and geographic variation of birds in body size and relative size of extremities, of size and shape of bill and wings, and on plumage colour, including the repeated emphasis on the gradual, i.e. clinal, nature of geographical character variation (Baird 1866, Allen 1871, 1875, 1876, 1877, Coues 1871, 1872, 1873, Ridgway 1872, 1873). In discussing certain aspects of plumage colour variation, Ridgway (1873: 549) referred in detail to some of the results of Gloger's (1833) early work.

W. Bock (pers. comm.) pointed out that the reason for the change in the thinking of North American ornithologists on the species concept probably developed from the very nature of the massive surveys of the American West, beginning with the early railroad surveys. These surveys were basically practical in nature, the goal being to investigate the potential of the vast areas of the west in order to make decisions on future uses of the land, e.g. for farming, grazing, etc, and hence the need to collect numerous geographical samples of animals and plants, as well as to collect large samples from each locality. These large collections of series of individuals of each species from numerous geographic localities established the foundation for the concept of geographic variation and of the subspecies concept, which had its major development among the North American ornithologists during the second half of the 19th century. Whereas topography, climate and animal populations change fairly gradually over large distances in Eurasia, animals and plants in the American West with its diverse terrain and climate are subdivided into numerous local forms, often with reasonably strong differences between the local populations. Hence the very nature of the material available to the American ornithologists for study permitted them to develop the subspecies concept quite easily.

There are interesting historical similarities between the coinciding taxonomic interpretations and the comparable application of fairly broad limits of morphospecies by the American ornithologists and by the earlier exploring ornithologists in Europe, arrived at independently by these 2 groups, although the researchers in North America were, of course, aware of many European publications. For example, several European articles and books are referred to in the 'Introductory Remarks' of Baird *et al.* (1860); the same was the case in the opposite sense, e.g. papers by S. F. Baird in 1866 and by Ridgway in 1879 were reissued in German during the same year of publication in the *Journal für Ornithologie*, where major ornithological books and articles were regularly and extensively reviewed; the same applies to *Ibis* in Britain. However, I did not find any evidence that the expedition reports of Nordmann, Middendorff, Schrenck and Radde were known in North America. The explanation for these similarities would seem to lie in the fact that both groups of ornithologists worked with ample specimen material (more extensive in the case of the North American workers) collected over large continental regions. Their analyses revealed several significant aspects of both individual and gradual geographical variation of bird species, and Rensch (1929b) later named after them certain regularities which they had discovered regarding the geographical variation of plumage colour and relative length of extremities (Gloger's and Allen's Rule, respectively). Although the North Americans were evolutionists considering species to be related to one another genealogically and the Europeans were creationists assuming an independent origin of each species, their taxonomic procedures were virtually identical; in other words, both groups were working under different theoretical species concepts but had developed comparable and broadly defined taxonomic species categories.

Like Gloger (1833) 40 years earlier, Allen (1871) also on the basis of his Lamarckian interpretation of geographical variation, suggested not recognizing subspecies names; but, as in Gloger's case, this proposal was not accepted by other ornithologists and Allen himself soon abandoned it, employing subspecies names routinely in subsequent years. In view of the discussion which soon developed in America and in Europe regarding the 'oversplitting' of species which vary gradually (clinally) over large regions (beginning with Allen 1890), it is surprising that no other method than the formal description of subspecies was proposed for the analysis of geographic variation of birds until several decades later (e.g. graphical mapping with the help of contour lines). The reason probably is that the 19th century ornithologists who employed trinomial nomenclature often treated 'subspecies' quite typologically, almost like a morphological species at a lower categorical rank (Mayr 1982: 289). The attitude of their minds was still conditioned to a taxonomy of discrete units and variation, and their nomenclature was based on it. However, the collecting of large numbers of specimens and their study in 'series' ('suites'), beginning in ornithology with the naturalists of the Gloger-Middendorff school and H. Schlegel in Europe and, in particular, with Agassiz (fishes), Baird, Coues, Allen, Ridgway and other ornithologists in North America, eventually led to the overcoming of the prevailing typological view of variation and the development of 'population thinking', which was "perhaps the greatest conceptual revolution that has taken place in biology" (Mayr 1963: 5).

The mission of Elliott Coues to London in July 1884 to propagate the application of wider species limits and the use of trinomials by European ornithologists failed completely. The opposition of zoologists at the British Museum was too strong (Sharpe 1884). Only Henry Seebohm, who was among Coues' audience, agreed with him. Seebohm had been influenced by Darwin's theories of evolution and by the work of the North American ornithologists. During his travels in Europe and Siberia, Seebohm had studied the intergradation of many so-called 'species' such as, e.g., *Sitta caesia*/*S. europaea* and *Corvus corone*/*C. cornix* (Seebohm 1882–1883: xi, 547, 1901: 500–504). In those years, only a few European ornithologists besides Seebohm (1882–1883, 1882) and Radde (1884) opposed the application of narrow species limits (e.g. Severzow 1873, Reichenow 1877, Berlepsch & Taczanowski 1883) until Victor von Tschusi (1890) in Austria also began to combine subspecies into wide morphospecies taxa following the principles of the North American workers, i.e. applying a truly trinomial nomenclature. On the other hand, a few European workers continued to designate subspecies with the old-fashioned expression 'var.' even into the present century (Dubois 1909, 1912). Tschusi (1890) believed that certain species characters are constant and others like colouration and colour pattern vary within rigid limits which variation cannot transgress. As discussed below, Seebohm's theoretical ideas were later to influence the development of the biological species concept in Europe when E. Hartert and O. Kleinschmidt entered the discussion during the 1890s.

The pre-Darwinian species concept of Otto Kleinschmidt (1870–1954)

In the tradition of the Gloger-Middendorff school as well as the work of H. Schlegel (1844a,b) and J. H. Blasius (1862) decades earlier (and long since largely forgotten*), Otto Kleinschmidt (1900, 1926) again emphasized a strongly typological-creationist theoretical species concept and formulated a broadly defined taxonomic species category. He thus delimited species taxa widely, combining weakly to strongly differentiated geographical forms in one unit, a "natural species" which he called "Formenkreis" (array of forms). His intention was to distinguish this assemblage from the monotypic Linnaean species of many contemporary museum ornithologists in Europe and to facilitate the application of this method also by those workers who did not want to abandon the narrow meaning of the term 'species' (Mayr 1942: 112). The component forms of a Formenkreis represent and more or less exclude one another geographically. Kleinschmidt gave each of his Formenkreise a new capitalized group name, e.g. *Parus Meridionalis* for the Marsh Tit (*P. palustris*) and *P. Salicarius* for the Willow Tit (*P. montanus*), to emphasize the difference between taxa of this broadly defined new taxonomic category and the taxa of the narrowly defined Linnaean species category. This procedure, although logical, is not acceptable under the rules of nomenclature and was followed by practically no other systematist.

---

*Although Kleinschmidt and several other ornithologists did mention incidentally some papers of these early workers, the relevance of the latters' arguments regarding a broadly defined taxonomic species category apparently was appreciated by only a few ornithologists (e.g. Hartert 1901: 216) in the discussions of microtaxonomic concepts around the turn of the century (see also below).

At the beginning of this century, Kleinschmidt's efforts, together with those of Ernst Hartert (see below), led to the replacement of the morphological species concept by the biological species concept in Europe, although Kleinschmidt's own theoretical views were basically pre-Darwinian and typological in nature. I emphasize, however, that most of the Formenkreise which he discussed in his monograph series 'Berajah' represent valid taxa (mostly species and superspecies) and many details of Kleinschmidt's methodology, such as his meticulous character analyses and his views on the importance of geographic representation, were highly influential during the first decades of this century (Stresemann 1936: 155, Mayr 1942: 112).

Like the workers of the Gloger-Middendorff school and the ornithologists in North America (e.g. Allen 1871: 186–250), Kleinschmidt documented important data on the individual and geographic variation of Palaearctic birds. His rediscovery of the specific distinctness of 2 sibling species of grey tits (*Parus montanus* and *P. palustris*) led him to emphasize repeatedly what Lamarck in 1786 had stated in these words: "Two species constantly distinct in reproduction sometimes offer less differences between them than do two varieties of the same species" (Burkhardt 1987: 163); similarly Darwin: "Hence species may be good ones and differ scarcely in any external character" (Notebook B: 213 cited in Mayr 1982: 266); and also Gloger (1856a,b: 283, 301). In discussing Kleinschmidt's concept of the Formenkreis, Hartert (1901: 216) compared it to the species notion of C. L. Gloger, J. H. Blasius and G. Radde. In a similar manner, Stresemann (1936: 154) emphasized that "There is not the slightest difference between his 'formenkreis' and the 'species' of Gloger and other Pre-Darwinists". Comparable to the views of these earlier workers, Kleinschmidt's theoretical species concept was typological-creationist and his taxonomic species category (Formenkreis) was broadly defined.

The typological nature of Kleinschmidt's theoretical viewpoint has been clearly recognized and specifically emphasized by several authors of the anti-Darwinian philosophical literature (Conrad-Martius 1938: 250ff, 1949, 1952) and of the creationist literature (Illies 1983: 118). The basic theoretical attitude of Otto Kleinschmidt (1870–1954) was probably determined by his religious commitments as a protestant pastor, his own claims to the contrary notwithstanding. Eck (1990: 62) stated similarly that Kleinschmidt's theoretical views (with roots outside the natural sciences) may have been influenced by his theological convictions. Under the guidance of his deeply religious mother and of several protestant teachers, he had decided to become a pastor when he was in his teens. His systematic work on birds (beginning in 1892 when he was a student of theology) was done against the background of a deeply religious world view. Kleinschmidt (1900) formulated his broadly conceived taxonomic species category of the Formenkreis after studying, during the 1890s, several geographically variable species (e.g. *Garrulus glandarius*), various sibling species ("parallel species", as he called them) in the genera *Parus, Certhia, Regulus* and the large falcons of the *Falco rusticolus* group. The Formenkreis as a taxonomic category was based on Kleinschmidt's typological-creationist theoretical species concept and his pre-existing religious attitude, through which he was sensitive to the theoretical implications of the specific distinctness of sibling species and the general lack of transitional forms between any of the sharply separated species that he studied. The discussions of Kleinschmidt's views by several recent biologists (Kelm 1960, Jahn *et al.* 1982: 540) seem biased due to an emphasis of certain selected ('modern') aspects of the theoretical basis of Kleinschmidt's work. For this reason, and in view of the historical importance of Kleinschmidt's interpretations, I present my analysis of his views in some detail below.

Like many pre-Darwinian systematists in Europe, Kleinschmidt (1900, 1926) taught that faunas are composed of "natural species", his Formenkreise. Each Formenkreis taxon is fairly uniform and sharply delimited like a crystal representing an independent unit from its beginning and with a separate "evolutionary" history. From his theoretical species concept he concluded that at the core of each Formenkreis (hidden behind the outside appearances of colouration and form) lies its essence (*sein Wesen*—Kleinschmit 1909: 1). Only the racial characters, not the essential characters, vary, causing the geographical differentiation of a Formenkreis (species). Individual variation of species characters resembles the regular and constant swinging of a pendulum. In Kleinschmidt's (1926: 109) words which characterize his theoretical species concept: "Each Formenkreis presumably had an independent area of origin, an independent time of origin and an independent process of formation (*Werdegang*) with an independent rate of transformation, in a word each had an independent world history (*Weltwerden*)." Kleinschmidt assumed that this is true even for very similar sibling species, e.g. Willow Tit *Parus montanus* and Marsh Tit *P. palustris* for which he stated (1921: 27): "And if the ancestors of *Parus Salicarius* and *Parus Meridionalis* once have been only two equal and microscopically small glass-clear droplets of protoplasma, they were two! (*sic*)" Even though Kleinschmidt assumed that the Formenkreise (species) underwent transformation through time and differentiated into varying numbers of geographical forms, the species had, in his view, no common history of branching evolution, each Formenkreis representing an independent "type".

Based on his superb knowledge especially of Palaearctic birds and applying the principles of his taxonomic species category of the Formenkreis, Kleinschmidt gathered related and geographically representative taxa in one Formenkreis. Due to his typological viewpoint, he placed all these taxa at the same low taxonomic level, designating them as subspecies trinomially despite their often drastically different taxonomic modification (weakly defined subspecies to vicariant species) and despite the peripheral range overlap of some representative forms, e.g. *Pluvialis apricaria*/*P. dominica, Uria lomvia*/*U. aalge, Picus major*/*P. syriacus, Luscinia* *megarhynchos/L. luscinia, Loxia pytyopsittacus/L. curvirostra/L. leucoptera, Passer domesticus/P. italiae/P. hispaniolensis*, and others. His broadly conceived taxonomic species category of the Formenkreis was, however, not precisely defined. In some Formenkreise, Kleinschmidt did distinguish between main or "capital" forms and subtle forms. In current terminology, Kleinschmidt included in one Formenkreis a monotypic species or a polytypic species, several vicariant biospecies of a superspecies or even a set of more distantly related and geographically representative species (e.g. the nutcrackers *Nucifraga caryocatactes—N. columbiana*, Hazel and Ruffed Grouse *Tetrastes bonasia—T. sewerzowi—T. umbellus* and the spruce grouse *Dendragapus falcipennis—D. canadensis*; see Eck 1970). Kleinschmidt's combining in one Formenkreis (species) even strongly differentiated and, in some cases, partially sympatric representatives (not very closely related biospecies) and still designating them trinomially as subspecies is understandable from the typological basis of his theoretical species concept, which led him to consider geographic character variation among representatives as rather superficial and comparatively minor, leaving the basic essence of a species untouched.

Although many of Kleinschmidt's Formenkreise represent polytypic biospecies and superspecies (Eck 1990), his taxonomic procedures led to strong objections by many contemporary ornithologists. Possibly to comply with some of these objections, Kleinschmidt (1940) distinguished, late in his life, more strongly differentiated "sectors" of a Formenkreis and more weakly differentiated "forms". At the same time (1941), he classified the Formenkreise into several different categories. Among German ornithological authors who followed Kleinschmidt's philosophy were, e.g., A. von Jordans, K. Meunier, H. Frieling and F. Peus.

Under his typologically conceived theoretical species concept and the broad taxonomic species category of the Formenkreis, Kleinschmidt outlined monophyletic taxa which, however, are not differentiated at the same level of the taxonomic hierarchy. Therefore, the Formenkreis is not directly comparable with any of the evolutionary taxonomic categories defined under the theoretical biospecies concept (species, superspecies, subgenus), although it comes close to, without being identical with, the "zoogeographical species" (Mayr & Short 1970) which comprises independent biospecies and superspecies. A similar composite of variously differentiated geographical representatives as the Formenkreis (occasionally with overlapping distributions of the component species) is the "*soort-complex*" (species complex) as traced among various groups of butterflies by Toxopeus (1930).

Further developments

In opposition to Kleinschmidt's and Hartert's views, the German ornithologists Count von Berlepsch (1898, 1911) and Reichenow (1901, 1911) abused, from the turn of the century, trinomial nomenclature in a very unusual manner (which was in contrast to their own previous practice since the 1870s). They applied trinomina to closely related geographical representatives, which they now, however, no longer considered as subspecies of a single species unit but as distinct, narrowly defined morphospecies ("conspecies"; not conspecies *sensu* Schlegel). They said that these separate species are similar morphologically to the binomially named species with which the "conspecies" are grouped (e.g. they can often be identified only with the help of comparative material). For this reason, Berlepsch and Reichenow objected strongly when Hartert (1897) proposed to duplicate the species name in nominate subspecies (also Lorenz 1892: 17). This taxonomic procedure, of course, demonstrated the subordination of subspecies under the species which was logical under Hartert's scheme but was impossible to accept under Berlepsch's and Reichenow's newly established notion of "conspecies".

During the first decades of this century, many North American ornithologists continued to adhere strictly to extant morphological intergradation as a necessary requirement in relating 2 geographically complementary forms as subspecies (Miller 1955). Intergradation was understood to comprise either gradual geographical blending of interconnected populations or overlapping of individual variation in geographically separated (allopatric) populations on islands or on the continent (Stone 1903, 1935, Grinnell 1918, 1921). The hybridizing woodpeckers *Colaptes auratus* and *C. cafer* continued to be considered as species, and Dwight (1918, 1925: 103) believed that species taxa possess intrinsic qualitative characters which he assumed are fundamental and constant. He further stated that these characters "underlie the other variations and determine, within specific limits, size, shape, pattern, and color." Species limits were drawn on the basis of morphological evidence and degrees of difference until Chapman (1924) suggested that each situation should be judged biologically on its own merits, thereby dismissing the exclusive application of the concept of morphological intergradation. In his extensive and meticulous work on African birds, Admiral Lynes (1926: 347) followed Chapman's principles of discriminating between species and subspecies of birds.

The broadly defined evolutionary-morphological taxonomic species category of more recent authors like Geyr (1924, 1929), Meinertzhagen (1928, 1951, 1954), and Eck (1985, 1988) leads to assemblages of phylogenetically related and vicariant forms which exhibit geographically orderly (directed) character transformation throughout the continuous or discontinuous distributional range of these assemblages. Genetic-reproductive isolation of 2 taxa in contact is not a species criterion under this view. Such broadly conceived morphological species taxa (Table 2) compare with zoogeographical species (Mayr & Short 1970). Following Kleinschmidt (1940), Eck (1985) designated sharply differentiated entities within widely delimited morphological species as "sectors".

THE ASCENT OF THE BIOLOGICAL SPECIES CONCEPT

Around the turn of the 18th and 19th centuries, several zoologists independently formulated definitions of the species which come quite close to that under the biological species concept of modern evolutionary biologists, although these early definitions were still conceived in a typological frame of mind (Mayr 1957, 1968). For example, G. Cuvier, in 1798, concluded: ". . . two wild forms which live at the same place in the same climate, without interbreeding, and always maintain their differences, have to be regarded as different species, no matter how trifling the difference might be" (Stresemann 1927, 1936). It has become known in recent years, that among those naturalists who conceived species biologically was Charles Darwin. During the late 1830s, upon the return from his expedition, he interpreted the basic taxonomic entity as biospecies (Kottler 1978, Mayr 1982: 266); but, during the 1850s, he returned to a morphological species concept. The malacologist Adolf Schmidt (1857: 6) stated that "forms which are repeatedly encountered living at the same locality without blending are to be considered as distinct species". To H. W. Bates (1862: 501), who explored the insect fauna of Amazonia, the criterion of true species was "when two or more of them are found coexisting in the same locality without intercrossing." Similarly, the entomologist Th. Eimer (1889: 16) said "species are groups of individuals which are so modified that successful interbreeding (with other such groups) is no longer possible."

Among the ornithologists of that period who fully endorsed Darwin's theories of evolution was Henry Seebohm in Britain who concluded (1882: 547): "The old definition of a species having lapsed, in consequence of the rejection of the theory of special creation, it is necessary to provide a new one. The first step toward an understanding of what constitutes a species is the admission of the existence of subspecies. Two forms which are apparently very distinct, as *Corvus corone* and *C. cornix* or *Carduelis major* and *C. caniceps*, are nevertheless found to be only subspecifically distinct—a complete series of examples from one extreme form to the other in each case being obtainable. These are produced by interbreeding." Seebohm was the first ornithologist to emphasize geographical isolation as the *sine qua non* for speciation to occur and he came close to a biological concept of species when he stated that in geographical isolation, the peculiarities of two forms may "become so far separated, that should their areas of distribution again overlap they will nevertheless not interbreed, and the two species may be considered to be completely segregated" (Seebohm 1881: x) and ". . . species are so completely differentiated . . . that they may inhabit the same area without any cross-breeding between them" (Seebohm 1887: 63). He also discussed geographical variation (as opposed to individual variation) as the basis for subspecies distinction and insisted that incipient species of birds exist in considerable numbers, as predicted by Darwin's theories of evolution. Seebohm voiced his opposition to the theoretical views of nearly all contemporary systematists in Britain with strong words suggesting, e.g., that they "be exiled to Siberia for a summer to learn to harmonise their system of nomenclature with the facts of nature" (Seebohm 1901: 503).

Many ornithologists during the 19th century tacitly applied the biological species concept in their studies of the natural history of local bird faunas without, however, discussing the theoretical basis of this concept. This was eventually done in explicit terms and with many details of its implications by two entomologists in Britain around the turn of the century, Karl Jordan (at Walter Rothschild's private museum in Tring near London) and Edward Poulton, the first zoologists to become fully aware of the biological basis for the distinctness of coexisting species (Mayr

1955, 1982). Their work was in the tradition of Darwin's and Wallace's concepts of gradual evolution and speciation through the differentiation of geographical subspecies. The results of their analyses completely contradicted the saltationist theories of speciation of the Mendelians at that time (Mayr 1980a). Jordan's ornithological colleague at Tring was Ernst Hartert who, under the influence of the work of Henry Seebohm (1882–1883, 1882, 1887) and of the ornithologists in North America, had, since the late 1880s, delimited species broadly, applying the concept of subspecies and trinomial nomenclature consistently (Hartert 1891 and several papers on tropical birds during the 1890s). Later on, Karl Jordan's influence is noticeable in Hartert's work (e.g. the subspecies definition of Hartert, 1903: vi, is basically that of Jordan in Rothschild & Jordan 1903: xlii). Hartert's contact with Kleinschmidt (Kelm 1960), in particular the latter's emphasis on geographical representation of allied forms, also was of importance. Ultimately, however, Hartert and Kleinschmidt disagreed over many issues which, I think, was mainly due to Kleinschmidt's typological viewpoint. Miriam Rothschild (1983) has written a fascinating biography of Lord Walter Rothschild, and an informative history of the Tring Zoological Museum with detailed chapters on its curators E. Hartert and K. Jordan. They were able to base their wide-ranging studies on large series of local populations of birds and insects, respectively, being the first naturalists-systematists fully to implement the biological species concept. In his *magnum opus* on the birds of the Palaearctic fauna (1903–1922), Hartert presented a list of the biological species of the avifauna of this large area judging allopatric forms on their own biological merits without feeling bound to the concept of morphological intergradation as still adhered to by many North American ornithologists. The latter agreed, however, with Hartert when he united a number of European and North American bird 'species' as conspecific, e.g. forms of *Podiceps grisegena, Branta bernicla, Melanitta fusca, Circus cyaneus, Accipiter gentilis,* and others. They disagreed, however, with Hartert's inclusion of, e.g., *Lanius ludovicianus* in *L. excubitor* and *Bombycilla cedrorum* in *B. garrulus*. On the other hand, Hartert retained species status for pairs like *Corvus c. corone* and *C. c. cornix* as well as for *Carduelis c. carduelis* and *C. c. caniceps* because, he said, these forms hybridize along only narrow zones and each form maintains its overall integrity and its morphologically distinct characters over most of its distributional range. Like most ornithologists during the late 19th century (e.g. Allen 1871, Elliot 1892), Hartert believed geographic variation is caused by direct influences of the environment, an interpretation that Heinroth (1903: 103), however, dismissed pointing out that the pattern of plumage colour is very similar in many related species which inhabit totally different climatic zones. In the case of adaptive colouration of birds of the deserts and polar regions, Heinroth assumed its origin through natural selection, as Newton (letter to Tristram dated 24 August 1858; see above). and Tristram (1859) had suggested decades earlier.

The work of the Tring scientists ushered in the end of the widespread application of the concept of narrow morphospecies in Europe. The new theoretical viewpoint and the use of trinomial nomenclature were here now seen as having originated in North America. As stated above, the work of the Gloger-Middendorff school was largely forgotten, which is not as surprising as it may seem considering the totally different, non-evolutionary, theoretical attitude of the members of that 'school'. The leading ornithologists at the large museums, e.g. Sharpe, Sclater and Reichenow, continued to resist the new trend for some years and published quite unfavourable reviews of Hartert's work (e.g. Sclater 1904). However, when Hartert, Jourdain, Ticehurst & Witherby issued 'A Handlist of British Birds' in 1912 (in which Hartert was responsible for the classification and nomenclature employed) the opposition was on the retreat. A few years later, the B.O.U. Committee preparing 'A List of British Birds' (1915) had already adopted trinomials. When the last volume of Hartert's 'Vögel der paläarktischen Fauna' was published in 1922, the application of his concepts of the taxonomic categories of species and subspecies had been generally adopted in Europe. In this intellectual struggle among European ornithologists of roughly 30 years duration, several other ornithologists had also joined forces with Hartert since the turn of the century, e.g. A. B. Meyer, L. Wiglesworth, C. E. Hellmayr, J. I. S. Whitaker and H. Schalow (Stresemann 1975). Among the latter, Meyer & Wiglesworth (1898) and Wiglesworth (1898) discussed several critical aspects of individual and geographic variation in southeast Asian birds, proposing informal designations for populations representing stages in stepped or continuous character clines (as we would say today). These authors introduced numbers and certain symbols (> and <) to designate plumage colour stages between formally named subspecies, of which the latter symbols have been applied by many later systematists.

Through the increased knowledge of geographical variation of birds, ornithologists had by then recognized that, in some species, the representative forms (subspecies) can be grouped in 2 or more subspecies groups, e.g. forms of the Hooded Crow and of the Carrion Crow within *Corvus corone* or forms of the *carduelis* subspecies-group and of the *caniceps* subspecies-group of *Carduelis carduelis*. This led to Laubmann's (1921, 1932) proposal of a rather cumbersome quadrinomial nomenclature which, although consistent with the hierarchical classification of microtaxonomic categories, did not find followers among ornithologists.

One side effect of the arguments on theoretical questions of the species concept and the taxonomic species category was that ornithologists had become overly preoccupied with subspecies taxa and had almost lost sight of the species taxa themselves in regional taxonomic surveys, which became in reality subspecies lists. This is as true for Hartert's work (1903–1922) on Palaearctic birds, where he treated monotypic species and all subspecies alike (numbering them consecutively from 1 to 2300*), as it is for the 4th edition of the A.O.U. Check-list (1931) and for Peters' 'Check-list of Birds of the World', which were also essentially lists of subspecies until Ernst Mayr assumed editorship of the Peters List with volume 9 (1960) and 'reintroduced', so to speak, the species as a unit symbolized by a binomial heading for each species taxon.

Ludwig Plate, a professor at Jena, was among those general biologists who, at the beginning of this century, defended the Darwinian theories of evolution against a growing opposition. In 1914, he conceived the species 'physiologically', stating that a species comprises all individuals which reproduce together sexually; a common bond between them facilitates mutual recognition and sexual reproduction; species taxa are real units in nature which exist independently of man. In North America, Taverner (1919) argued, in dismissing the morphospecies concept of C. H. Merriam, "the species is a definite entity and its essential character is its genetic isolation. Absence of intergradation with other forms is the only test of the species as it exists at present. There is a barrier that isolates modern specific groups one from another . . .". In the case of allopatric forms, "the possibility of intergradation . . . must necessarily be estimated under the guidance of what evidence we have." Also for Chapman (1924) "proof of distinctness of two or more forms is their occurrence together when breeding without intergradation." He confirmed that there are many species which are more similar to each other than are many subspecies of the same species. The taxonomic rank of geographically isolated taxa is to be estimated by inference, he said.

---

*Notice Hartert's (1922 (3): vi) correction of his numbering species and subspecies from no. 2100 onward.

POPULATION SYSTEMATICS

Population systematics or the 'new systematics' steadily gained influence worldwide under the leadership of Stresemann, Rensch and Mayr during the 1920s, 1930s and 1940s. The emphasis was on the biological species concept and on a fairly broadly defined multidimensional taxonomic species category. Species taxa were seen as aggregates of populations which often vary clinally. Character gradients (clines; Huxley 1938a,b, 1939)* of a species may run in different directions and a 'subspecies' may belong to more than one cline. Not even the most extreme splitting will lead to homogeneous 'sub-subspecies' of clinally varying species. Morphological, ethological, physiological, biochemical, and bioacoustic characters and their geographical variation were investigated in ever increasing detail. Phenomena studied were the population continuum, zones of secondary intergradation, and geographical isolates. The publications of Rensch (1929b, 1934) and Mayr (1942) were the first comprehensive statements of this new research tradition which was soon to unify most or all systematists worldwide, including those outside the field of ornithology, and which, from the late 1930s through the 1940s, merged with population genetics and palaeontology in the synthetic theory of evolution (Mayr & Provine 1980).

During the 1920s and 1930s, Erwin Stresemann contributed extensively to a clarification of the biological species concept and a meaningful delimitation of species taxa through his many perceptive theoretical discussions of systematic concepts, thus building an important conceptual basis during the preparatory phase of the evolutionary synthesis. Although he was an evolutionist from the beginning of his scientific career in about 1910, Stresemann was influenced at first by some of the systematic principles of Kleinschmidt, but soon built on the views of E. Hartert and L. Plate (1914). As early as 1919, Stresemann adopted a biological species concept as it became standard in evolutionary biology in later decades (Mayr 1942: 119, 1957: 17, 1980b: 96, 1982: 273): "Forms which have reached the species level have diverged physiologically to the extent that, as proven in nature, they can come together again without interbreeding . . . morphological divergence is independent of physiological divergence" (Stresemann 1919a: 64, 66). "Forms which can maintain themselves separate without interbreeding when living together under natural conditions are considered as distinct species" (Stresemann 1920: 152). In the case of allopatric taxa, their rank as subspecies or species is to be determined by inference based upon several auxiliary criteria (degree of similarities in morphology, ecology, voice, etc.; overlap of the ranges of individual variation; comparison with comparable congeneric forms which are in contact and either do or do not interbreed). For several years, however, Stresemann continued to assign species taxa to a very broadly defined taxonomic category of biospecies. In 1925 and 1926, he recognized the existence of biospecies which replace each other geographically without or only rarely hybridizing along their contact zone. This discovery of closely related and geographically representative biological species (currently called allospecies and paraspecies) led Stresemann to accept Rensch's (1928) proposal to distinguish between polytypic species (*Rassenkreis*) and superspecies (*Artenkreis*)—see Haffer (1991) for further details. In later years, Stresemann delimited species more narrowly than before (see Table 2) and investigated the ecological segregation of closely allied biospecies (Stresemann 1943). He had interpreted the origin of species through allopatric speciation already in 1913 and, during subsequent years, he investigated 'mutations' as one possible mechanism of genetic change (Stresemann 1926). Chapman (1923, 1928) held a similar view but ascribed clinal character variation to direct environmental influence.

---

*As shown in previous pages, gradual geographical variation of species had already been discussed briefly by Gloger (1833) for Eurasian birds and, more extensively, by Allen (1871) and other ornithologists for North American birds as well as by Wiglesworth (1898) and Meyer & Wiglesworth (1898) for southeast Asian birds. Reinig (1938a) analyzed numerous "character progressions" in Palaearctic birds and other animals. These authors, however, usually intended to solve certain taxonomic problems rather than to study independent character clines present in species populations.

In contrast to this latter interpretation held by a majority of ornithologists at the beginning of this century, Stresemann (1919a,b,c) applied an historical interpretation to the phenomenon of clinal geographic variation. In several conspicuous subspecies pairs of European birds (*Aegithalos caudatus, Corvus corone, Sitta europaea, Pyrrhula pyrrhula*), Stresemann postulated a postglacial contact of forms which had differentiated in geographical isolation during preceding glacial periods of the Pleistocene, leading to introgressive hybridization and to the development of the observed smooth geographical character gradients. This work was originally stimulated by Kleinschmidt's (1911) discussion of geological factors in the distribution of European birds (Udvardy 1992), as well as by the early articles of Seebohm (1882) on interbreeding between forms of crows, shrikes and goldfinches, and those of Berlepsch (1885), who had discussed the hybridization between the eastern and western subspecies of the Long-tailed Tit.

Bernhard Rensch was a student at Halle during the early 1920s, and at that time visited the nearby home of Otto Kleinschmidt (Rensch 1979), who demonstrated to him the relations of many representative forms on the basis of his large private collection of birds. At the same time, Rensch worked temporarily at the Zoological Museum in Berlin with E. Stresemann who, in 1925, saw to it that Rensch was employed by this institution (Rensch 1979: 49). Influenced by Stresemann's work on geographically representative biospecies, Rensch soon revised Kleinschmidt's terminology. In 1926, he introduced the term '*Rassenkreis*' (array of races) to replace Kleinschmidt's term '*Formenkreis*' (Rensch 1926: 254). The latter term appeared to Rensch misleading because of its prior use by zoologists to designate groups of closely related species regardless of whether they were allopatric or sympatric. Although the term Formenkreis (Kleinschmidt) and Rassenkreis (Rensch) were indeed synonymous in Rensch's (1926) first article, at the International Ornithological Congress in Copenhagen (May 1926) he in fact had mentioned that a Formenkreis may comprise one or several Rassenkreise (Rensch 1929a). In 1928, he coined the term *Artenkreis* (translated into superspecies by Mayr 1931) for a complex of 2 or more vicariant Rassenkreise (Rensch 1928, 1929). Since these latter publications, the terms Rassenkreis and Formenkreis are no longer synonyms, a fact overlooked by some authors until today. The 'Genus geographicum' and the 'geospecies' (Rensch 1931: 464) are synonyms of 'superspecies' and biospecies, respectively; neither of them corresponds to the term zoogeographical species (Mayr & Short 1970). Rensch (1929b: 14) originally restricted the use of the term 'species' to monotypic species taxa, designating polytypic species as Rassenkreise. This distinction was not accepted by other authors, because it became obvious that these designations referred to different kinds of species taxa rather than to different taxonomic categories. The terms monotypic and polytypic species were introduced by Huxley (1938, 1939) independently of J. A. Allen (1910), who had used them quite freely in his review of the 3rd edition of the 'Check-list of North American birds'.

The discovery of geographically representative forms which do not or only rarely hybridize along their zones of contact (Fig. 2) and, therefore, represent biological species (Rensch 1928, 1929), eventually led to a reversal of the excessive 'lumping' tendency among ornithologists which had reached a peak in Europe under the influence of Kleinschmidt's views: e.g. several publications by Stresemann during the early 1920s (see Haffer 1991), as well as some of Hellmayr's (*Catalogue of Birds of the Americas*—1924–1942) and Stegmann's (1934, 1935) papers on broadly circumscribed species. These authors used trinomial nomenclature for the purpose of expressing genetic relationships, also of non-intergrading representatives which, in some cases, exhibit different habitat preferences near the contact zones (see also comments by Meise 1938). The occurrence of vicariant biospecies with contiguous ranges, currently called parapatric species, demonstrated that caution must be exercised when combining as conspecific representative forms with adjoining or allopatric ranges. In a comprehensive study of the climatic rules of geographic variation and of population systematics, Rensch (1929b, 1934) showed that the concepts of polytypic species and superspecies are applicable to most groups of vertebrate and invertebrate animals worldwide. He abandoned his Lamarckian interpretation of the origin of geographical variation during

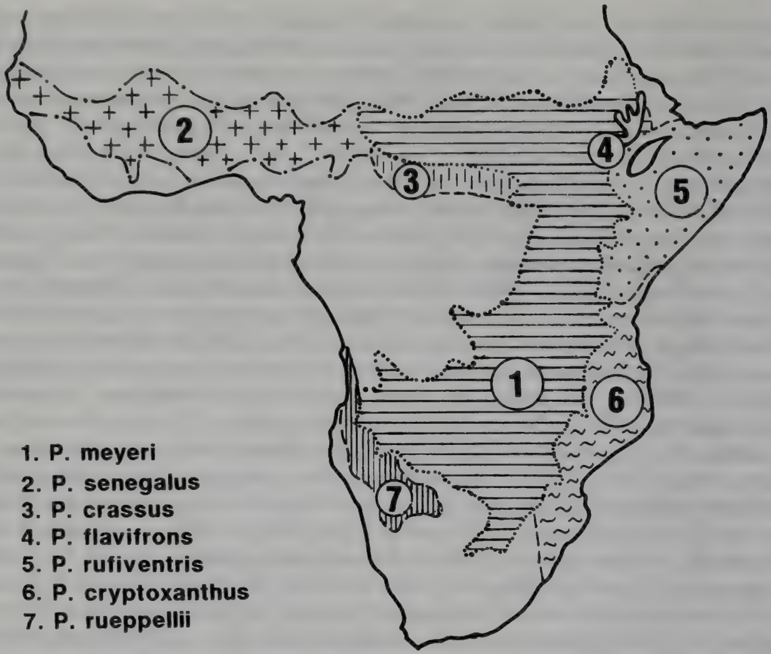


Figure 2. Distribution of the African parrots of the *Poicephalus meyeri* superspecies. Simplified after Snow (1978). This assemblage of parapatric species was used by Rensch (1928), together with other evidence, to discuss the occurrence of vicariant biospecies.

the early 1930s when be became familiar with the new redefinition of mutation as slight genetic variations which could respond to natural selection.

In North America, the systematic principles of both Hartert and Chapman regarding the ranking of taxa as subspecies and species were increasingly applied in their work by the leading ornithologists of the 1920s and 1930s, e.g. J. Chapin, R. C. Murphy, J. L. Peters, L. Griscom and many others who were also influenced by the new concepts of genetics and evolution. Chapin (1932) warned against the hasty lumping of geographic representatives under a binomial name to include groups that may have diverged to a point beyond the possibility of intergradation. He emphasized the genetic basis of slight subspecific differences knowing that "environment selects, rather than directs the variations".

Building on the work of Stresemann and of Rensch, Mayr (1942, 1963, 1970) prepared several major critical syntheses of the systematic, genetic and ecological aspects of biological species and an analysis of the speciation process. Thus he established the theoretical biological species concept in all its ramifications, based on which he defined the multi-dimensional species category within taxonomy. Through his contributions, the biospecies concept became one of the central tenets of the modern synthetic theory of evolution during the 1940s and 1950s, a fact too well-known to be discussed here in any detail. Lack (1944, 1949, 1971) added important data on the ecological aspects of the speciation process, as acknowledged by Mayr (1982: 274). Niche differentiation must be complete for 2 species to be able to occupy the same habitat. Therefore, several different situations may arise if species come into secondary contact (Lack 1944): (1) One species eliminates the other because it is so much better adapted ecologically, or (2) one species will exclude the other in part of its range with a narrow or broad zone of overlap developing where both are about equally well adapted; (3) the 2 forms will occupy separate but adjacent habitats in the same region of overlap; (4) both species are similar ecologically and occupy adjacent geographical regions excluding each other along the zone of contact due to ecological competition (parapatry in current terms) or (5) both species become sympatric and syntopic because they are ecologically fully isolated. Lack concluded that ecological divergence between forms must have been initiated when they were isolated from each other geographically, although it may have been intensified after they met.

In several historical essays, Mayr (1980a,b, 1988) discussed the role of systematics in the evolutionary synthesis, in particular the contributions made by naturalists-systematists (since about 1900) regarding the development of population thinking, the quantitative analysis of gradual adaptive geographic variation, and the importance of geographical speciation. Selander (1971) critically reviewed modern studies on the systematics and speciation process in birds published during the 1950s and 1960s.

In recent years, Stepanyan (1974, 1978) delimited the species of Palaearctic birds on the basis of a narrow species notion, often designating entities as species that other authors consider subspecies or megasubspecies under the biological species concept.

PHYLETIC LINEAGES AS ‘SPECIES’

Morphological-biological changes along phyletic lineages through time occur slowly (‘gently’) or more or less abruptly. However, even ‘abrupt’ shifts or changes along lineages with or without lineage splitting, are continuous and ‘gradual’, merely occurring at a higher rate than other lineages changes over time which occur at a slower rate (see Fig. 1). Shifts along lineages which may or may not be accompanied by splitting events (speciation) are taken by many palaeontologists to subdivide a given lineage into portions considered as ‘species’ in the time dimension. On the other hand, cladists subdivide lineages exclusively at splitting events regardless of whether considerable morphological-biological shifts have occurred along only one or both lineages at the time of the splitting event (Willmann 1983, 1985). Since there is no method of subdividing the evolutionary continuum of phyletic lineages in a meaningful and non-arbitrary manner, it appears best to restrict the theoretical concept of species to particular time levels (whose ‘duration’ will have to be defined) and to speak of phyletic lineages in the time dimension. A separate taxonomy for such lineages outside the Linnaean system of genera and species should be designed.

Species taxa based upon morphological analyses of fossil specimens may or may not correlate with reproductive communities (biological species). In morphologically well differentiated groups, species probably often refer to taxa below the level of biospecies, whereas in morphologically (osteologically) uniform groups such as, e.g., salamanders or certain groups of songbirds, a fossil species probably comprises a group of closely allied biological species.

In a very perceptive early remark, Neumayr (1889: 67) was insisting that the concept of species, as derived from observations of extant faunas, cannot be applied to phyletic lineages. "However", he continued, "if we take a particular (form) by itself without regard to the other members of its lineage and consider only its relations to contemporary organisms, then indeed this form is a good species. As soon as we take into consideration the entire phyletic lineage of which this form is a part, nothing exists which would correspond to a species. The species concept cannot be applied when reasonably complete paleontological material is available and must disappear from the realm of paleontology." Similarly, Simpson (1943: 171) stated: "Clearly a species as a subdivision of a temporal, or vertical, succession is quite a diffent thing from a species as a spatial, or horizontal, unit and cannot be defined in the same way. The difference is so great and, to a thoughtful paleozoologist, so obvious that it is proper to doubt whether such subdivisions should be called species and whether vertical classification should not proceed on an entirely different plan from the basically and historically horizontal Linnean system. So far none of the varied proposals for non-Linnean arrangement and nomenclature has been widely accepted and none seems promising at present."

Despite this early advice (see also Sylvester-Bradley 1956, Simpson 1961, Reif 1984) palaeontologists and cladists continue to discuss 'species' concepts that refer to differently delimited portions of phyletic lineages. Hopefully, further discussions will lead to a clarification of the issues involved.

An early attempt at analyzing 'vertical' genealogical relations among extant taxa at the level of subspecies and species was made by Reinig (1938a,b, 1939a,b), who wisely used a new terminology for the entities he delimited in his studies (contrasting them to Rensch's terms of monotypic and polytypic species). Considering the postglacial expansion of birds from postulated glacial refugia in the Holarctic Region, Reinig traced genealogical units ("Sippe") on the basis of his analyses of geographical character gradients (determining character polarity on the basis of the assumed direction of range expansion from the refugia). A genealogical unit embraces all those populations ("Kleinsippe", geographical subspecies) that are morphologically and geographically differentiated (diagnosable) and "which are interrelated in such a way that each single group can be derived phylogenetically with the aid of morphological characteristics and historical and chorological knowledge from the group immediately adjacent to it" in the direction of the Pleistocene refuge area, where the expansion of the genealogical unit presumably had started (Reinig 1939a: 23). He felt that many species of the Palaearctic fauna may not represent evolutionary communities, i.e. be monophyletic in a cladistic sense, and explained that his term 'Sippe' (genealogical unit) has no definite taxonomic rank lying outside the customary categories of species and subspecies. Eller (1939, 1940) applied Reinig's methods to an analysis of the genealogy of geographical subspecies of the *Papilio machaon* group of butterflies. Reinig did not, however, provide examples at the species level to illustrate the differences between his approach and the application of the concept of biospecies. Non-hybridizing genealogical units in contact (paraspecies) are designated also by Reinig with a Linnaean binomen (species). He preferred to combine allopatric genealogical entities in loosely defined Formenkreise *sensu* Kleinschmidt. Reinig's rather unfortunate terminology of "Sippen" was 'preoccupied' by botanical usage and by the 19th-century natural philosopher Lorenz Oken who had suggested to replace the term genus by "Sippe".

More recent analyses of the 'vertical' (historical) relationships of groups of reptile populations at the infraspecific level are those of Böhme (1978) and Thorpe (1984).

Species limits under the cladistic species concept range from fairly wide (Hennig 1966, Willmann 1983, 1985, 1986) to narrow (Cracraft 1983, McKitrick & Zink 1988). Hennig and many other cladists delimit extant species basically following the criteria of the multidimensional species category. These latter systematists consider it inappropriate to enquire whether species are monophyletic, paraphyletic or polyphyletic, claiming that these terms apply only to groups of species (but see De Queiroz & Donoghue 1988, McKitrick & Zink 1988 and further discussions in *Cladistics* 5, 1989 and 6, 1990). On the other hand, cladists applying narrow species limits under the concept of the phylogenetic species (Cracraft 1983) assign species status to any population that is morphologically diagnosable (which basically renders this concept, in an operational, not theoretical, sense comparable to the monotypic morphological concept of 19th-century systematists). These cladists are concerned that paraphyletic and polyphyletic taxa may be ranked as species if medium-wide and wide species limits are applied.

A biological species becomes paraphyletic when a daughter species originated through 'budding' (Fig. 3); e.g., a derivative population of a widespread mainland species may have reached species status on a nearby island. However, this speciation event had no effect on the parental biospecies (no. 3, Fig. 3) on the mainland from which neospecies 4 has budded off. The mainland species (no. 3) is real in the sense that it represents a biological unit characterized by close genetic-reproductive and ecological relations among its component subspecies taxa. Traditionally, such biological clusters have been designated as 'species'. They would be in need of another categorical name if the term 'species' was to be transferred to the lower taxonomic level of the basic component morphotaxa (subspecies). The cladistic analyses schematically illustrated in Fig. 3 (if feasible at that infraspecific level) yield relevant phylogenetic ('vertical') and biogeographical data on the origin of the various groups of taxa. However, transfer and application of the term 'species' to phylogenetic lineages within biospecies would confuse the issue. Cracraft (1983) and other cladists suggest that each of the 9 lineages illustrated in Fig. 3 should be considered as species, regardless of their forming 4 separate clusters through genetic cohesion and intergradation.

Several large sample studies of birds should be undertaken to determine approximately what percentage of biospecies are monophyletic entities and how many species are paraphyletic or polyphyletic taxa.

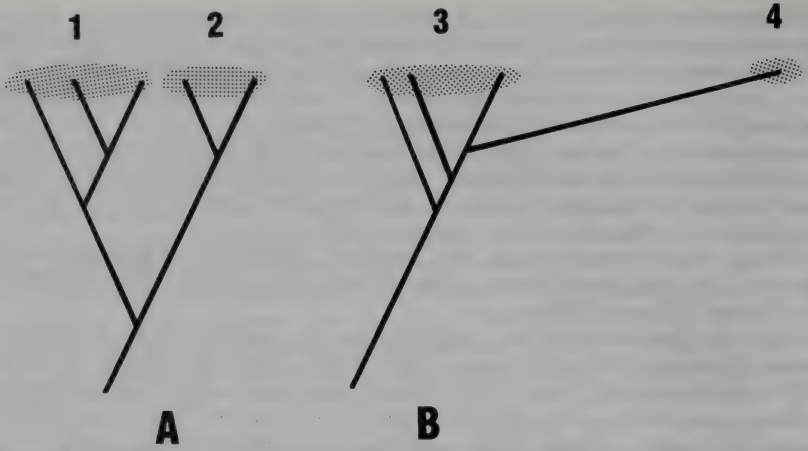


Figure 3. Speciation through splitting (A) and budding (B) resulting in monophyletic biospecies 1 and 2 (consisting of 3 and 2 subspecies, respectively) and paraphyletic biospecies 3 (3 subspecies). Species 4 which budded off from species 3 is monotypic and may demonstrate its species status by occurring sympatrically with some or all subspecies of species 3. Shading indicates genetic cohesion and intergradation of subspecies along contact zones.

McKitrick & Zink (1988: 8) believe that "many if not most biological species probably are monophyletic" and Szalay & Bock (1991: 35) are of the opinion that probably "many species" are paraphyletic. It would indeed be an important task to analyze phylogenetic lineages at intraspecific levels in the world's avifauna in order to understand the phylogenetic relations of as many component taxa of biological species as possible and to study their biogeographical history.

Geneflow among contiguous conspecific populations may prevent a meaningful cladistic analysis for many such taxa to be carried out. It would appear, therefore, that, among infraspecific entities, acceptable results of cladistic studies can be expected only for allopatric taxa and, in the case of contiguous populations, when these represent well differentiated (mega)subspecies characterized by morphological traits that can be assumed are not easily affected by geneflow.

THE CHANGING NUMBERS OF BIRD SPECIES

Because of the different opinions among ornithologists as to the circumscription of species taxa, i.e. their application of different taxonomic species categories, a higher or lower number of bird species has been recognized at all times. These different counts refer to the birds of the world as a whole, of a large continental region or an archipelago, though not to the number of bird species at a single locality which, of course, coincides under the various taxonomic categories of species discussed. Ornithologists applying a narrow morphological species category in taxonomy arrived at high numbers of species which, during the last century, were rapidly increasing due to the continuous discovery and description of new forms made known through numerous scientific expeditions (Fig. 4). On the other hand, ornithologists following the

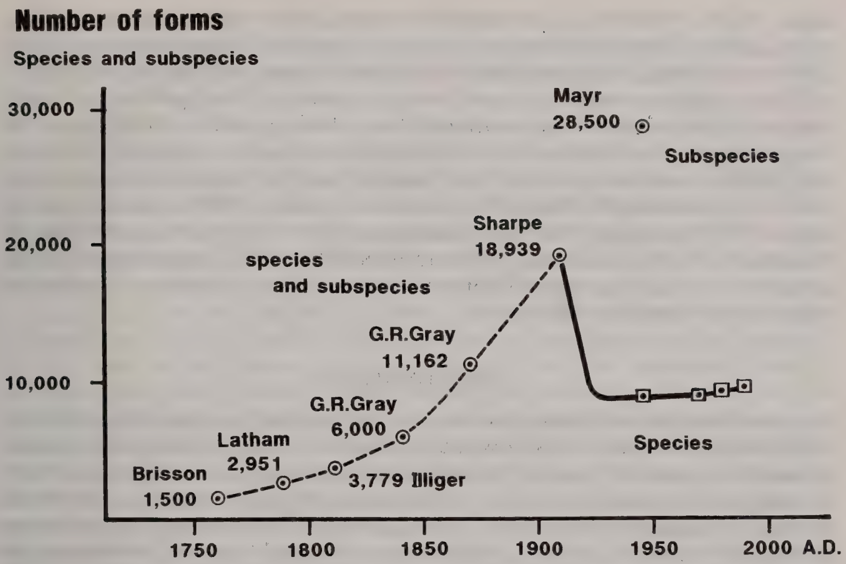


Figure 4. Increase of the number of species and subspecies of birds known during the last 250 years. Application of the multidimensional species concept (under the theoretical concept of the biological species) shortly after the end of the 19th century caused a conspicuous decrease in the number of species taxa recognized, a development which was stopped during the late 1920s when geographically representative biospecies were discovered. Data are from Stresemann (1975), Bock & Farrand (1980) and Sibley & Monroe (1990).

principles of the Gloger-Middendorff school in Europe and of the Bairdian school in North America recognized considerably fewer species; others arrived at an intermediate number. Whereas in North America the situation regarding intermediate species limits remained quite stable into the 20th century, a narrow monotypic species category was applied by the leading museum ornithologists in Europe toward the end of the 19th century resulting in the recognition of high numbers of species taxa, mainly through the influence of the authoritative 'Catalogue of the Birds in the British Museum' (27 volumes, 1874–1898). This trend culminated when R. B. Sharpe published his 'A Hand-list of the Genera and Species of Birds' (1899–1909) recognizing 18,939 species (many of which represent allospecies and subspecies).

During the following 20 years, the situation reversed itself entirely. Numerous Linnaean morphospecies were reinterpreted as subspecies and combined in more widely conceived biological species taxa. The result was a precipitous decline in the number of species recognized (Fig. 4). Several authors went too far in 'lumping' geographically representative forms into species units. This trend was eventually halted by warning voices from North America (e.g. Ridgway 1924, Swarth 1931, Chapin 1932, Stone 1935, Grinnell 1935) and especially by Rensch's (1928, 1929) emphasis on the existence of closely related allopatric and parapatric species (together forming a superspecies). A period of moderate stability regarding species numbers followed during the late 1930s and early 1940s when Mayr (1946: 68) estimated the total number of known birds to be 8616 species. A gentle increase of species numbers began during the late 1940s when many geographically isolated representatives were reinterpreted as species and combined in superspecies. This 'quiet revolution' (Mayr 1980b) at the microtaxonomic level during the last 30–40 years led to a continuous increase in the number of bird species, only slightly boosted by the discovery of genuine new biospecies (153 species from 1938 to 1985—Vuilleumier & Mayr 1987): Bock & Farrand (1980) counted a world total of 9021 species (3747 nonpasserines, 5274 passerines) and Sibley & Monroe (1990) 9672 species (3960 nonpasserines, 5712 passerines). In the latter species list, superspecies are indicated to give a measure of ecological units in the world's avifauna.

DISCUSSION

A consideration of reproductive communities (biospecies) refers to 'horizontal' relationships of extant populations or of contemporary populations at particular time levels in the geological past. On the other hand, tracing evolutionary descent of populations refers to a study of 'vertical' phyletic lineages (not 'species') through time. This contrasting and complementary way of looking at the 'horizontal' and 'vertical' relationships of taxa is reminiscent of a fundamental distinction made by several biologists and philosophers of the late 18th century, although details of these schemes are not directly comparable.

G. L. de Buffon distinguished from after 1740 a 'real' (physical) ordering of concepts and an 'abstract' ordering, thus viewing the taxonomic problem, in the first case, in terms of history and genealogy and, in the second case, in terms of morphology and character resemblance. He understood the different category levels—species, genera, orders, etc.—in 2 ways, in one as 'abstract' entities of reason, and in the other as grounded in the succession of real time and space in the Leibnizian understanding of those concepts (Sloan 1979: 117). Somewhat later, 1775–1788, Immanuel Kant distinguished in a similar way horizontal, a-temporal *Naturbeschreibung* (description of nature) and vertical, temporal *Naturgeschichte* (history of nature). Both Buffon and Kant related the recognition of natural species to the historical unity of the stem dividing animals according to genealogy (with reference to reproduction) rather than on the basis of morphological character resemblance (logical or morphological species of Linnaean taxonomy). All animals which generate fertile young with each other belong to a physical species.

Buffon's concepts, as clarified and to some extent reinterpreted by Kant, were made, in 1796, by Christoph Girtanner the basis of an appeal for a new and generalized research programme in natural history: an inquiry into the temporal and genealogical relations of life was to be separated from the traditional taxonomic and morphological approach. However, Girtanner's proposal had little impact on contemporary systematic studies and the writings of influential authors. Johann Blumenbach during the 1790s emphasized morphological aspects (the *habitus*) and Carl Illiger in 1800 shifted ambiguously from the domain of Naturgeschichte to Naturbeschreibung (Sloan 1979: 143).

My review of theoretical species concepts and of narrow to wide taxonomic species categories as applied by ornithologists over the last 200 years indicates that the basic questions, as in other branches of science as well, had been formulated already by the early pioneers (Haffer 1990). Throughout the 19th century, controversies persisted among ornithologists advocating wide or narrow species limits based on interbreeding and morphological considerations, respectively. The 'horizontal' biological species concept (Mayr 1942) was accepted by a majority of systematists during the first half of this century. Explicitly genealogical considerations were introduced later by Willy Hennig (1950, 1966) in his historical analyses of species populations based on cladistic methods.

Application of a narrowly defined taxonomic species category led systematists to assign species status to the smallest diagnosable taxa and, in this way, to emphasize nature's diversity at low taxonomic levels; whereas the delimitation of wide biogeographical species taxa (superspecies and independent species) stresses the recognition of ecological units in the world's fauna (Bock & Farrand 1980). The definition of the biological species category takes into consideration the most significant microtaxonomic event, i.e. the attainment of genetic isolation by a group of populations; consequently, biospecies are delimited as genetically closed reproductive communities at intermediate levels of microtaxonomic differentiation.

A practical application of a narrow, morphologically defined taxonomic species category (e.g. the cladistic concept of 'phylogenetic species') would result in an enormously increased number of taxonomic species compared to that currently recognized under the multidimensional taxonomic species category. On the other hand, application of the category of the wide biogeographical species would lead to a reduction of the number of presently recognized species. The approximately 9600 known extant biological species of birds (Sibley & Monroe 1990), according to 2 estimates, form 5000–6000 biogeographical species (Bock & Farrand 1980) or 7000 ± 200 biogeographical species (Mayr 1980b). These current issues in systematic ornithology represent the latest reformulation of ancient questions which have been discussed intensively throughout the nineteenth century and before.

All levels of differentiation at which species limits have been proposed are biologically significant. It will be advisable, therefore, that these stages of increased microtaxonomic differentiation are taken into consideration by identifying and listing the subspecies groups (megasubspecies, i.e. 'phylogenetic species'), the biological species and the biogeographical species in the world's avifaunas. In this way, the conceptual relations among these taxonomic categories and their component taxa may be studied, and the various entities may be used in analyses of the biogeographical and phylogenetic history as well as the ecological divergence of genera and families of birds.

Acknowledgements

I am very grateful to Ernst Mayr (Cambridge, Massachusetts) for information on several points discussed in this article and for his critical review of this manuscript. W. J. Bock (New York) discussed with me the theory of species concepts; I gratefully acknowledge his detailed review of this manuscript and his important suggestions for improvement. S. Eck

(Dresden), H. Pieper (Kiel) and the late H. E. Wolters also read a first draft and suggested various useful amendments. In Bonn, I thank R. van den Elzen, K. Schuchmann, G. Rheinwald, C. Naumann, W. Böhme and C. Häuser for occasional discussions and for their permission to use the collections and libraries of the Alexander Koenig Museum at any time. The following persons kindly supported my work by providing various information, loan of publications and access to their personal or institutional libraries: E. Bezzel (Garmisch-Partenkirchen), H. Engländer (Köln), the late H. Kelm, A. Kleinschmidt (Wolfenbüttel), M. Louette (Tervuren), G. Mauersberger (Berlin), J. Neumann (Neubrandenburg), D. S. Peters (Frankfurt), W.-D. Reif (Tübingen), H. Ringleben (Bremen), R. Schlenker (Radolfzell,) and B. Stephan (Berlin).

Summary

The theoretical concept of the biological species and the multidimensional species category, as currently applied by a majority of ornithologists and by many other biologists, replaced the typological-morphological species concept during the first half of this century and became a central tenet of the synthetic theory of evolution. The concept of biospecies is a 'horizontal' concept referring to contemporary reproductive communities at any particular period, e.g. the Recent period or any other time level of the geological past. Historical 'species' concepts as applied by cladists and palaeontologists refer to artificially delimited portions of 'vertical' phyletic lineages for which the application of the term 'species' causes severe problems. Discussions would be simplified if the concept and term 'species' was to be restricted to cross sections of phyletic lineages at any time level and a separate taxonomy outside the Linnaean system of genera and species was to be conceived to deal with phyletic lineages. Under each of the theoretical species concepts, species taxa are assigned broadly to intermediate or narrowly defined taxonomic species categories.

Ornithologists of the 19th century applied morphological species concepts, emphasizing morphological character differences between species (rather than distinctness) and the fertility of conspecific individuals (rather than the isolation from non-conspecific populations). Nearly all leading museum ornithologists in 19th-century Europe delineated monotypic Linnaean species, whereas the explorer-naturalists of the Gloger-Middendorff school (including Pallas, Faber, Gloger, Nordmann, Middendorff, Schrenck, Radde, as well as Schlegel and Blasius) delimited widely circumscribed species taxa. Their researches in the vast territories of eastern Europe, Siberia and the Far East from the late 18th century to the 1880s and, in particular, their rich specimen material, demonstrated direct intergradation of many taxa (geographical varieties) of birds, thus revealing the conspecific nature of numerous narrowly conceived morphospecies previously described by museum workers. The ornithologists of the Gloger-Middendorff school also studied several conspicuous phenomena of geographical character variation in birds (and mammals) across Eurasia, especially plumage colouration (and pelage) and body size, but none of them was an evolutionist. They all adhered to a typological-creationist theoretical species concept. During the late 19th century, the museum specialists' taxonomic notion of narrow morphospecies dominated systematic ornithology in Europe, overtaking the work of the naturalists of the Gloger-Middendorff school, which fell into oblivion.

The ornithologists of the Bairdian school in North America (Baird, Coues, Allen, Ridgway) further developed the concept of subspecies after the 1850s and especially from the 1870s onward. Their views were fully in accord with Darwin's theories of evolution; thus they defined the subspecies in a somewhat simplified manner as 'nascent species'. These ornithologists were able to base their studies on collections of extensive specimen material which they had obtained during a series of exploring expeditions across the North American continent. Their studies led to the discovery of many aspects of both individual and geographic variation in birds.

There are interesting historical similarities between the coinciding taxonomic interpretations and the comparable application of fairly broad limits of morphospecies by the North American ornithologists and the earlier exploring ornithologists in Europe, arrived at independently by these research groups. The study of specimens in 'series' ('suites'), beginning with the naturalists of the Gloger-Middendorff school and, in particular, with the naturalists of the Bairdian school in North America, eventually led to the overcoming of the prevailing typological view of variation and the development of 'population thinking'.

Influenced by the work of Henry Seebohm in Britain and that of the North American ornithologists, Hartert in England and Kleinschmidt in Germany jointly succeeded in overcoming the strong opposition of the leading ornithologists in Europe during the 1890s and early 1900s and introduced a concept which soon developed into the biological species concept through the work of Stresemann, Rensch, and in particular, Ernst Mayr.

Hopefully, ornithologists will continue the study of taxa at low, intermediate and high levels of microtaxonomic differentiation and will identify the subspecies groups, biological species and the biogeographical species in the world's avifaunas. Cladistic analyses will provide historical ('vertical') overviews of phyletic lineages at different taxonomic levels.

References:

Allen, J. A. 1871. On the mammals and winter birds of east Florida, with an examination of certain assumed specific characters in birds, and a sketch of the bird faunae of eastern North America. *Bull. Mus. Comp. Zool.* 2: 161–450.

— 1875. Geographical variation in North American birds. *Proc. Boston Soc. Nat. Hist.* 15: 212–219.

— 1876. Progress of ornithology in the United States during the last century. *Amer. Naturalist* 10: 536–550.

— 1877. The influence of physical conditions in the genesis of species. *Radical Rev.* 1: 108–140. Reprinted in *Ann. Rep. Smiths. Inst. for 1905* 1906: 375–402. Washington 1906.

— 1890. To what extent is it profitable to recognize geographical forms among North American birds? *Auk* 7: 1–9.

— 1908. Another aspect of the species question. *Amer. Naturalist* 42: 592–600.

— 1910. Review of the A.O.U. Check-List of North American Birds, 3rd edition. *Auk* 27: 466–472.

Amadon, D. 1966. The superspecies concept. *Syst. Zool.* 15: 245–249.

— 1968. Further remarks on the superspecies concept. *Syst. Zool.* 17: 345–346.

Amadon, D. & Short, L. L. 1976. Treatment of subspecies approaching species status. *Syst. Zool.* 25: 161–167.

American Ornithologists' Union. 1886. *Code of Nomenclature and Check-list of North American Birds*. 1st edition.

— 1931. *Check-list of North American Birds*. 4th edition.

Baird, S. F. 1866. The distribution and migrations of North American birds. *Amer. J. Sci.* 41: 78–90, 184–192, 337–347.

Baird, S. F., Brewer, T. M. & Ridgway, R. 1874. *A History of North American Birds. Land Birds*, 2 vols. Boston. Reprint edition, Arno Press, New York, 1974.

—, —, — 1884. *The Water Birds of North America*, 2 vols. *Mem. Mus. Comp. Zool.* 12.

Baird, S. F., Cassin, J. & Lawrence, G. N. 1860. *The Birds of North America*, 2 vols. Philadelphia. Reprint edition, Arno Press, New York. 1974.

Baldamus, E. 1861. Ornithologische Reiseskizzen vom Jahre 1860. *J. Ornith.* 9: 60–64.

Bates, H. W. 1862. Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidae. *Trans. Linn. Soc. London* 23: 495–566.

Berlepsch, H. von. 1885. [Hybridization in Long-tailed Tits]. *J. Ornith.* 33: 17–18.

— 1898. Ueber den Begriff der Subspecies und Nomenclaturfragen. *Abhandl. Ber. Zool. Anthropol.–Ethnogr. Mus. Dresden* 7: 18–20.

— 1911. Revision der Tanagriden. *Bericht über den V. Intern. Orn.–Kongr. (Berlin 1910):* 1001–1161.

Berlepsch, H. von & Taczanowski, L. 1883. Liste des oiseaux recueillis par MM. Stolzmann et Siemiradzki dans l'Ecuadeur occidentale. *Proc. Zool. Soc. London*: 536–577.

Blasius, J. H. 1844. *Reise im europaeischen Russland in den Jahren 1840 und 1841*, 2 vols. Braunschweig, Westermann.

— 1857. *Naturgeschichte der Säugethiere Deutschlands*. Braunschweig, Vieweg & Sohn.,

— 1858. Einige Bemerkungen über Beständigkeit und Schwanken der Speciescharaktere. *Naumannia* 8: 243–251.

— 1861. On the diversity in the estimate of the European ornis, and its causes. *Ibis* 3: 292–302.

— 1862. *A List of the Birds of Europe*. Norwich, Matchett & Stevensen. London, Trübner & Co.

Blyth, E. 1850. Remarks on the modes of variation of nearly affined species or races of birds, chiefly inhabitants of India. *J. Asiatic Soc.* 19: 221–229.

Bock, W. J. 1979. The synthetic explanation of macroevolutionary change—a reductionistic approach. *Bull. Carnegie Mus. Nat. Hist.* 13: 20–69.

— 1986. Species concepts, speciation, and macroevolution. Pp. 31–57 *in* K. Iwatsuki, P. H. Raven and W. J. Bock (eds), *Modern Aspects of Species*. Tokyo, Univ. Tokyo Press.

Bock, W. J. & Farrand, Jr., J. 1980. The number of species and genera of Recent birds. *Amer. Mus. Nat. Novit.* No. 2703.

Böhme, W. 1978. Das Kühnelt'sche Prinzip der regionalen Stenözie und seine Bedeutung für das Subspezies-Problem: ein theoretischer Ansatz. *Z. Zool. Syst. Evolut.-forsch.* 16: 256–266.

Brehm, C. L. 1823. *Lehrbuch der Naturgeschichte aller europäischen Vögel.* Erster Theil. Jena.

— 1831. *Handbuch der Naturgeschichte aller Vögel Deutschlands.* Ilmenau.

Burkhardt, F. 1982. Darwin and the biological establishment. *Biol. J. Linn. Soc.* 17: 39–44.

Burkhardt, Jr., R. W. 1987. Lamarck and species. Pp. 161–180 *in* J.-L. Fischer and J. Roger (eds) *Histoire du concept d'espèce dans les sciences de la vie.* Fondation Singer-Polignac, Paris.

Bush, G. L. 1975. Modes of animal speciation. *Annual Rev. Ecol. Syst.* 6: 339–364.

Chapin, J. P. 1932. *The Birds of the Belgian Congo.* Part I. *Bull. Amer. Mus. Nat. Hist.* 65.

Chapman, F. M. 1923. Mutation among birds in the genus *Buarremon. Bull. Amer. Mus. Nat. Hist.* 48: 243–278.

— 1924. Criteria for the determination of subspecies in systematic ornithology. *Auk* 41: 17–29.

— 1928. Mutation in *Capito auratus. Amer. Mus. Novit.* No. 335.

Cohen, I. B. 1985. Three notes on the reception of Darwin's ideas on natural selection (Henry Baker Tristram, Alfred Newton, Samuel Wilberforce). Pp. 589–607 *in* D. Kohn (ed.) *The Darwinian Heritage.* Princeton.

Coleman, W. 1979. Bergmann's Rule: Animal heat as a biological phenomenon. *Stud. Hist. Biol.* 3: 67–88.

Committee of the Brit. Ornith. Union. 1915. *A List of British Birds.* 2nd and revised edition. London.

Conrad-Martius, H. 1938. *Ursprung und Aufbau des lebendigen Kosmos.* Müller, Salzburg, Leipzig.

— 1949. *Abstammungslehre.* München, Kösel.

— 1952. Das Artproblem in naturphilosophischer Beleuchtung. *Experientia* 8: 400–404.

Coues, E. 1871. Progress of American ornithology. *Amer. Naturalist* 5: 364–373.

— 1872. *Key to North American Birds.* New York.

— 1873. Color-variation in birds dependent upon climatic influences. *Amer. Naturalist* 7: 415–418.

— 1874. *Birds of the Northwest*: A Hand-book of the Ornithology of the Region drained by the Missouri River and its Tributaries. Washington.

— 1884. On the application of trinomial nomenclature to zoology. *The Zoologist* 8: 241–247.

— 1903. *Key to North American Birds.* 5th edition. Boston. Reprint edition, Arno Press, New York. 1974.

Cracraft, J. 1983. Species concepts and speciation analysis. *Curr. Ornith.* 1: 159–187.

— 1984. The terminology of allopatric speciation. *Syst. Zool.* 33: 115–116.

Cutright, P. R. & Brodhead, M. J. 1981. *Elliott Coues. Naturalist and Frontier Historian.* Urbana, Univ. Illinois Press.

De Queiroz, K. & Donoghue, M. J. 1988. Phylogenetic systematics and the species problem. *Cladistics* 4: 317–338.

Donoghue, M. J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. *The Bryologist* 88: 172–181.

Dubois, A. 1871. *Conspectus Systematicus & Geographicus Avium Europaearum.* Bruxelles.

— 1873. De la variabilité de certains oiseaux et indication de quelques espèces nouvelles pour l'Europe. *Rev. Magasin de Zoologie* 3 sér., T. 1er (no. 11): 386–399.

— 1909–1910. Réflexions sur l'espèce en ornithologie. *Rev. Franc. d'Orn.* 1: 113–115; 2: 119–122.

— 1912. Nouvelle revue des oiseaux en Belgique. *Mém. Soc. Zool. France* 25: 162–209.

Dwight, J. 1918. The geographical distribution of color and of other variable characters in the genus *Junco*: a new aspect of specific and subspecific values. *Bull. Amer. Mus. Nat. Hist.* 38: 269–309.

— 1925. The gulls (*Laridae*) of the world; their plumage, moults, variations, relationships and distribution. *Bull. Amer. Mus. Nat. Hist.* 52: 63–401.

Eck, S. 1970. Verzeichnis der Formenkreis-Namen Otto Kleinschmidts mit Bemerkungen zur Formenkreis-Nomenklatur. *Zool. Abhandl. Mus. Tierk. Dresden* 31: 85–137.

— 1985. Katalog der ornithologischen Sammlung Dr. Udo Bährmanns (6. Fortsetzung). *Zool. Abhandl. Mus. Tierk. Dresden* 41: 1–31.

Eck, S. 1988. Gesichtspunkte zur Art-Systematik der Meisen (Paridae). *Zool. Abhandl. Mus. Tierk. Dresden* 43: 101–134.

— 1990. Ist Otto Kleinschmidts Formenkreis-Konzept wieder aktuell? *Current Topics in Avian Biology. Proc. Int. DO-G Meeting (Bonn 1988)*: 61–67.

Eimer, G. H. T. 1889. *Die Artbildung und Verwandtschaft bei den Schmetterlingen.* Jena.

Eldredge, N. & Cracraft, J. 1980. *Phylogenetic Patterns and the Evolutionary Process.* New York, Columbia Univ. Press.

Eller, K. 1939. Fragen und Probleme zur Zoogeographie und zur Rassen- und Artbildung in der *Papilio machaon*-Gruppe. *Verhandl. VII Intern. Kongr. Entomologie* 1: 74–101.

— 1940. Zur Genealogie geographischer Rassen. *Forsch. Fortschr.* 16: 68–71.

Elliot, D. G. 1892. The inheritance of acquired characters. *Auk.* 9: 77–104.

Faber, F. 1825-1826. *Über das Leben der hochnordischen Vögel.* Leipzig.

Farber, P. L. 1982. *The Emergence of Ornithology as a Scientific Discipline: 1760–1850.* Dordrecht, Reidel.

Frost, D. R. & Hillis, D. M. 1990. Species in concept and practice: herpetological applications. *Herpetologica* 46: 87–104.

Gadow, H. 1883. Cichlomorphae. *Catalogue of Birds in the Collection of the British Museum.* Vol. 8. London.

— 1884. Nectariniidae and Meliphagidae. *Catalogue of Birds in the Collection of the British Museum.* Vol. 9. London.

Gage, A. T. & Stearn, W. T. 1988. *A Bicentenary History of the Linnaean Society of London.* Academic Press, London.

Gebhardt, L. 1964. Die Ornithologen Mitteleuropas. Ein Nachschlagewerk. Giessen, Brühl. Band 2–4. *J. Ornith.* 111 (1970), 115 (1974), 121 (1980), Sonderhefte.

Geyr von Schweppenburg, H. 1924. Anmerkungen zur Subspeziesfrage. *Zool. Jb. Syst.* 49: 131–196.

— 1929. Sollen wir den Subspeziesbegriff streng geographisch umgrenzen? *Verhandl. VI. Intern. Ornith.-Kongr. (Kopenhagen 1926)*: 84–88.

Gillispie, C. C. (ed.). 1970–1980. *Dictionary of Scientific Biography.* Vol. 1–16. New York, Scribner.

Gittenberger, E. 1972. Zum Artbegriff. *Acta Biotheoretika* 11: 47–62.

Gloger, C. L. 1833. *Das Abändern der Vögel durch Einfluss des Klima's.* Breslau.

— 1834. *Vollständiges Handbuch der Naturgeschichte der Vögel Europa's, mit besonderer Rücksicht auf Deutschland.* Erster Theil (Landvögel). Breslau.

— 1856a. Ueber den Begriff von 'Art', ['species'] und was in dieselbe hinein gehört. *J. Ornith.* 4: 260–270.

— 1856b. Ueber Grundsätze zur Beurtheilung wirklicher Arten und blosser Abänderungen. *J. Ornith.* 4: 271–300 (also *Naumannia* 6: 277–307).

Gould, J. 1855. [On geographical colour differences in birds]. *Proc. Zool. Soc. London* 23: 77–78.

Grant, P. R. 1986. *Ecology and Evolution of Darwin's Finches.* Princeton.

Grant, P. R. & Grant, B. R. 1992. Hybridization of bird species. *Science* 256: 193–197.

Grinnell, J. 1918. Concerning a certain tendency in systematic ornithology. *Auk* 35: 505–507.

— 1921. The criterion for the trinomial. *Auk* 38: 469–470.

— 1935. Review of Hellmayr's Part VII of the 'Catalogue of Birds of the Americas'. *Condor* 37: 90–92.

Haffer, J. 1986. Superspecies and species limits in vertebrates. *Z. Zool. Syst. Evol. Forsch.* 24: 169–190.

— 1990. Ornithologists and species concepts. *Proc. Intern. 100th DO-G Meeting. Current Topics in Avian Biology* (Bonn 1988): 57–60.

— 1991. Artbegriff und Artbegrenzung im Werk des Ornithologen Erwin Stresemann (1889–1972). *Mitt. Zool. Mus. Berlin 67, Suppl.* (*Ann. Orn.* 15): 77–91.

Hall, E. R. 1981. *The Mammals of North America.* 2nd edition. Vol. 2. New York, Wiley.

Hartert, E. 1891. *Katalog der Vogelsammlung* im Museum der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main. Frankfurt.

— 1897. Über Begriff und Nomenclatur subspecifischer Formen nebst Bemerkungen über die Nomenclatur der Familien. *Zool. Anz.* 20: 41–46.

— 1901. Über die Bedeutung der Kleinschmidt'schen Formenkreise. *J. Ornith.* 49: 210–220.

— E. 1903–1922. *Die Vögel der Paläarktischen Fauna.* 3 Vols. Berlin.

Hartert, E., Jourdain, F. C. R., Ticehurst, N. F. & Witherby, H. F. 1912. *A Hand-List of British Birds*. London.

Hartlaub, G. 1865. Bericht über die Leistungen in der Naturgeschichte der Vögel während des Jahres 1864. *Arch. Naturgesch.* 31: 1–28.

Heinroth, O. 1903. Ornithologische Ergebnisse der 'I. Deutschen Südsee-Expedition von Br. Mencke'. *J. Ornith.* 51: 65–125.

Hennig, W. 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin.

— 1966. *Phylogenetic Systematics*. Urbana, Univ. Illinois Press.

Hensel, R. 1861. Bericht über die Leistungen in der Naturgeschichte der Säugethiere während des Jahres 1859. *Arch. Naturgesch.* 26: 19–69.

Hofsten, N. von. 1916. Zur älteren Geschichte des Diskontinuitätsproblems in der Biogeographie. *Zool. Annalen* 7: 197–353.

Homeyer, E. von. 1868–1870. Beiträge zur Kenntnis der Vögel Ostsibiriens und des Amurlandes. *J. Ornith.* 16: 197–206, 248–259, 17: 48–61, 119–125, 169–174, 18: 56–64, 161–176, 421–438.

Hume, A. O. 1875. What is a species? *Stray Feathers* 3: 257–262.

Huxley, J. S. 1938a. Clines: an auxiliary taxonomic principle. *Nature* (London) 142: 219–220.

— 1938b. Species formation and geographical isolation. *Proc. Linn. Soc. London* 150: 253–264.

— 1939. Clines: an auxiliary method in taxonomy. *Bijdragen tot de Dierkunde* (Leiden) 27: 491–520.

Illies, J. 1983. *Der Jahrhundert-Irrtum. Würdigung und Kritik des Darwinismus*. Frankfurt am Main, Umschau Verlag.

Jahn, I., Löther, R. & Senglaub, K. 1982. *Geschichte der Biologie*. Jena, Fischer.

Jerdon, T. C. 1862. *The Birds of India*. Vol. 1 (Reprint edition, Dehra Dun, India, 1982).

Kelm, H. 1960. Otto Kleinschmidt und Ernst Hartert. Aus ihrem Briefwechsel 1895–1932. *J. Ornith.* 101: 404–471.

Kleinschmidt, O. 1900. Arten oder Formenkreise? *J. Ornith.* 48: 134–139.

— 1909. *Corvus Nucifraga*. Berajah, Zoographia infinita. Halle.

— 1911. Über die europäischen Blaukehlchen. *Verhandl. V. Intern. Orn. Congr. (Berlin 1910)*: 283–287.

— 1921. *Parus Salicarius*. Berajah (Zoographia Infinita), 1912–1937. Gebauer-Schwetschke, Halle.

— 1926. Die Formenkreislehre und das Weltwerden des Lebens. Halle. (Engl. transl. by Rev. F. C. R. Jourdain: 'The Formenkreis Theory and the Progress of the Organic World. A re-casting of the theory of descent and race-study to prepare the way for a harmonious conception of the universal reality'. London, H. F. & G. Witherby, 1930).

— 1940. *Corvus albus* und seine Verwandten. *Falco* 36: 17–22.

— 1941. Welche Folgerungen ergeben sich aus C. L. Brehms Feststellung von Doppelgruppen der Baumläufer, Graumeisen und Haubenlerchen für die Erforschung der exotischen Tierwelt? *Falco* 37: 6–12.

Kottler, M. J. 1978. Charles Darwin's biological species concept and theory of geographic speciation: the transmutation notebooks. *Ann. Sci.* 35: 275–297.

Lack, D. 1944. Ecological aspects of species-formation in passerine birds. *Ibis* 86: 260–286.

— 1949. The significance of ecological isolation. Pp.299–308 *in* G. L. Jepsen, E. Mayr and G. G. Simpson (eds) *Genetics, Paleontology and Evolution*. Princeton.

— 1971. *Ecological Isolation in Birds*. Oxford, Blackwell Sci. Publ.

Laubmann, A. 1921. Die quaternäre Nomenclatur und ihre Anwendung in der Ornithologie. *Jaarber. Club Nederl. Vogelk.* 11: 40–50.

— 1932. Des fins et du but de la nomenclature quadrinominale. *Alauda*, ser. 2 (4): 375–389.

Lorenz, L. von. 1892. Diskussion über die bisherigen Versuche zur Regelung der zoologischen Nomenklatur. *Verhandl. Zool.-Bot. Ges. Wien, Stizungsber.* 42: 12–23.

Lynes, H. 1926. On the birds of North and Central Darfur. Taxonomic Appendix. Part I. *Ibis* 12th ser. (2): 346–405.

Mayr, E. 1931. Birds collected during the Whitney South Sea expedition XII. Notes on *Halcyon chloris* and some of its subspecies. *Amer. Mus. Novit.* No. 469.

— 1942. *Systematics and the Origin of Species from the Viewpoint of a Zoologist*. New York, Columbia Univ. Press.

— 1946. The number of species of birds. *Auk* 63: 64–69.

— 1955. Karl Jordan's contribution to current concepts in systematics and evolution. *Trans. Roy. Entomol. Soc. London* 107: 45–66.

Mayr, E. 1957. Species concepts and definitions. Pp. 1–22 *in* E. Mayr (ed.) *The Species Problem.* Amer. Assoc. Adv. Sci., Washington. Reprint edition, Arno Press, New York, 1974.

— 1963. *Animal Species and Evolution.* Cambridge, Mass., Harvard Univ. Press.

— 1968. Illiger and the biological species concept. *J. Hist. Biol.* 1: 163–178.

— 1969. *Principles of Systematic Zoology.* New York, McGraw-Hill.

— 1970. *Populations, Species, and Evolution.* Cambridge, Mass. Harvard Univ. Press.

— 1980a. The role of systematics in the Evolutionary Synthesis. Pp. 123–136 *in* E. Mayr and W. B. Provine (eds) *The Evolutionary Synthesis.* Cambridge, Mass., Harvard Univ. Press.

— 1980b. Problems of the classification of birds, a progress report. *Acta XVII Congr. Intern. Orn. (Berlin 1978)*: 95–112. Berlin, Deutsche Orn.-Gesellschaft.

— 1982. *The Growth of Biological Thought.* Cambridge, Mass., Harvard Univ. Press.

— 1987. The species as a category, taxon and population. Pp. 303–320 *in* J.-L. Fischer and J. Roger (eds) *Histoire du concept d'espèce dans les sciences de la vie.* Paris, Fondation Singer-Polignac.

— 1988. The contributions of birds to evolutionary theory. *Acta XIX Congr. Intern. Orn.* Vol. 2: 2718–2723.

Mayr, E. & Provine, W. B. (eds). 1980. *The Evolutionary Synthesis. Perspectives in the Unification of Biology.* Cambridge, Mass., Harvard Univ. Press.

Mayr, E. & Short, L. L. 1970. Species taxa of North American Birds. A contribution to comparative systematics. *Publ. Nuttall Orn. Club* No. 9.

McKitrick, M. C. & Zink, R. M. 1988. Species concepts in ornithology. *Condor* 90: 1–14.

Mearns, B. & Mearns, R. 1988. *Biographies for Birdwatchers. The Lives of Those Commemorated in Western Palearctic Bird Names.* London, Academic Press.

Meinertzhagen, R. 1928 Some biological problems connected with the Himalaya. *Ibis* 12th ser., vol. 4: 480–533.

— 1951. Some relationships between African, Oriental, and Palaearctic genera and species, with a review of the genus *Monticola. Ibis* 93: 443–459.

— 1954. *Birds of Arabia.* London, Oliver & Boyd.

Meise, W. 1938. Fortschritte der ornithologischen Systematik seit 1920. *Proc. 8th Int. Orn. Congr. (Oxford 1934)*: 49–189.

Merriam, C. H. 1897. Suggestions for a new method of discriminating between species and subspecies. *Science* N.S. 5: 753–758.

Meyer, A. B. & Wiglesworth, L. W. 1898. *The Birds of Celebes and the Neighbouring Islands.* Vol. 1. Friedländer, Berlin.

Middendorff, A. Th. von. 1853. *Wirbelthiere; Säugethiere, Vögel und Amphibien. Sibirische Reise, Band II, Theil 2.* St Petersburg.

— 1867. *Die Thierwelt Sibiriens. Sibirische Reise, Band IV, Theil 2, erste Lieferung.* St Petersburg.

— 1874. *Die Thierwelt Sibiriens (Schluss). Sibirische Reise, Band IV, Theil 2, zweite Lieferung.* St Petersburg.

Miller, A. H. 1955. Concepts and problems of avian systematics in relation to evolutionary processes. Pp. 1–22 *in* A. Wolfson (ed.) *Recent Studies in Avian Biology.* Urbana, Univ. Illinois Press.

Mishler, B. D. & Brandon, R. N. 1987. Individuality, pluralism, and the phylogenetic species concept. *Biol. Philos.* 2: 397–414.

Mullens, W. H. & Swann, H. K. 1917. *A Bibliography of British Ornithology.* London, Macmillan.

Nelson, G. & Platnick, N. 1981. *Systematics and Biogeography. Cladistics and Vicariance.* Columbia Univ. Press, New York.

Neumayr, M. 1889. *Die Stämme des Thierreiches.* Wirbellose Thiere. Wien, Tempsky.

Newton, A. 1896. *A Dictionary of Birds.* London, Adam & Black.

Nordmann, A. von. 1840. *Observations sur la Faune Pontique.* Voyage dans le Russe Méridionale et la Crimée, par la Hongrie, la Valachie et la Moldavie, executé en 1837, sous la direction de M. Anatole de Demidoff. Vol. 3. Paris, Bourdin.

Pallas, P. S. 1811. *Zoographia Rosso-Asiatica.* St Petersburg.

Panov, E. N. 1989. *Natural Hybridisation and Ethological Isolation in Birds.* Nauka, Moscow.

Paterson, H. E. H. 1985. The recognition concept of species. Pp. 21–29 *in* E. S. Vrba (ed.) *Species and Speciation.* Transvaal Mus. Monogr. No. 4, Pretoria.

Peters, D. S. 1970. Über den Zusammenhang von biologischem Artbegriff und phylogenetischer Systematik. Aufsätze und Reden Senckenb. *Naturf. Gesellschaft* 18, 39 pp.

Plate, L. 1914. *Prinzipien der Systematik mit besonderer Berücksichtigung des Systems der Tiere.* Pp. 92–164 *in* R. Hertwig & R. von Wettstein (eds) *Abstammungslehre, Systematik, Paläontologie, Biogeographie.* Die Kultur der Gegenwart, Teil 3, 4. Abt., 4. Band. Leipzig, Teubner.

Prigogine, A. 1980. Etude de quelques contact secondaires au Zaire oriental. *Gerfaut* 70: 305–384.

— 1984a. Speciation problems in birds with special reference to the Afrotropical Region. *Mitt. Zool. Mus. Berlin 60, Suppl.* (Ann. Orn. 8): 3–27.

— 1984b. Secondary contacts in central Africa. *Proc. V. Pan-Afr. Orn. Congr.* 81–96.

Radde, G. 1862. *Die Säugethierfauna. Reisen im Süden von Ost-Sibirien in den Jahren 1855–1859.* Band I. St Petersburg.

— 1863. *Die Festlands-Ornis des südöstlichen Sibiriens. Reisen im Süden von Ost-Sibirien in den Jahren 1855–1859.* Band II. St Petersburg.

— 1884. *Ornis Caucasica.* Kassel, Fischer.

Reichenow, A. 1877. Systematische Uebersicht der Schreitvögel (Gressores). *J. Ornith.* 25: 113–171, 225–277.

— 1880. Die wissenschaftlichen Benennungen der Vögel. *Orn. Centralblatt* 5: 25–27, 68–69, 156–159, 164–166.

— 1893. System und Genealogie. *Orn. Monatsber.* 1: 113–117, 133–136.

— 1901. Über Begriff und Benennung von Subspecies. *Orn. Monatsber.* 9: 145–149.

— 1911. Über die Fortschritte und den gegenwärtigen Stand der Ornithologie. *Ber. V. Int. Orn.-Kongr. (Berlin 1910)*: 117–132.

— 1913. *Die Vögel. Handbuch der Systematischen Ornithologie.* Band 1. Stuttgart, Enke.

Reif, W.-E. 1984. Artabgrenzung und das Konzept der evolutionären Art in der Paläontologie. *Z. Zool. Syst. Evol. Forsch.* 22: 263–286.

Reinig, W. F. 1938a. *Elimination und Selektion.* Jena, Fischer.

— 1938b. On the history of Holarctic floral and faunal habitats in the Quaternary period. *Research and Progress* 4: 67–72.

— 1939a. Real systematic units in zoology and their genetic structure. *Research and Progress* 5: 20–39.

— 1939b. Die genetisch-chorologischen Grundlagen der gerichteten geographischen Variabilität. *Z. Ind. Abst. Vererbungslehre* 76: 260–308.

Remane, J. 1985. Der Artbegriff in Zoologie, Phylogenetik und Biostratigraphie. *Paläontol. Z.* 59: 171–182.

Rensch, B. 1926. Rassenkreisstudien bei Mollusken I. Der Rassenkreis der Felsenschnecke *Campylaea zonata* Studer. *Zool. Anzeiger* 67: 253–263.

— 1928. Grenzfälle von Rasse und Art. *J. Ornith.* 76: 222–231.

— 1929a. Die Berechtigung der ornithologischen systematischen Prinzipien in der Gesamtzoologie. *Verhandl. VI. Int. Orn.-Kongr. (Kopenhagen 1926)*: 228–242.

— 1929b. *Das Prinzip geographischer Rassenkreise und das Problem der Artbildung.* Berlin, Borntraeger.

— 1931. Die Vogelwelt von Lombok, Sumbawa und Flores. *Mitt. Zool. Mus. Berlin* 17: 451–637.

— 1934. *Kurze Anweisung für Zoologisch-Systematische Studien.* Leipzig, Akad. Verlagsgesellschaft.

— 1979. *Lebensweg Eines Biologen in Einem Turbulenten Jahrhundert.* Stuttgart, Fischer.

Ridgway, R. 1872–1873. On the relation between color and geographical distribution in birds, as exhibited in melanism and hyperchromism. *Amer. J. Sci. & Arts,* 3rd ser., vol. 4: 454–460, 5: 39–44.

— 1873. The relation between the color and the geographical distribution of birds. *Amer. Naturalist* 7: 548–555.

— 1879. On the use of trinomials in zoological nomenclature. *Bull. Nuttall Orn. Club* 4: 129–134.

— 1881. Nomenclature of North American Birds. *Bull. U.S. National Mus.* 21: 1–94.

— 1901. *The Birds of North and Middle America.* Vol. 1.

— 1924. A plea for caution in use of trinomials. *Auk* 40: 375–376.

Rothschild, M. 1983. *Dear Lord Rothschild. Birds, Butterflies and History.* London, Hutchinson.

Rothschild, W. & Jordan, K. 1903. A revision of the lepidopterous family Sphingidae. *Novit. Zool.* 9, Suppl.

Schlegel, F. 1867. Das Leidener Museum. *Zool. Garten* 8: 201–208.

Schlegel, H. 1844a. *Kritische Übersicht der Europäischen Vögel*. Leiden.
— 1844b. *Aves*. *In* C. J. Temminck & H. Schlegel *Fauna Japonica*. Leiden.
— 1854–1858. *De Vogels van Nederland*. 2 vols.
Schmidt, A. 1857. *Die Kritischen Gruppen der Europäischen Clausilien*. Leipzig, Costenoble.
Schrenck, L. von. 1859. *Säugethiere des Amur-Landes*. Reisen und Forschungen im Amur-Lande in den Jahren 1854–1856. Band 1, erste Lieferung. St Petersburg.
— 1860. *Vögel des Amur-Landes*. Reisen und Forschungen im Amur-Lande. Band 1, zweite Lieferung. St Petersburg.
Sclater, P. L. 1896. Remarks on the divergencies between the 'Rules for naming Animals' of the German Zoological Society and the Stricklandian Code of Nomenclature. *Proc. Zool. Soc. London*: 306–319.
— 1904. Hartert on the Palaearctic Avifauna. *Ibis* 8th ser., vol. 4: 291–293.
Seebohm, H. 1881. Turdidae. *Catalogue Birds Brit. Mus.* Vol. 5. London.
— 1882. On the interbreeding of birds. *Ibis* 4th ser., vol. 6: 546–550.
— 1882–1883. *A History of British Birds*. Vol. 1. London.
— 1887. *The Geographical Distribution of the Family Charadriidae*. London.
— 1901. *The Birds of Siberia*. A record of a naturalist's visits to the valleys of the Petchora and Yenesei. Murray; reprint edition A. Sutton, Dursley, 1976.
Selander, R. K. 1971. Systematics and speciation in birds. Pp. 57–147 *in* D. S. Farner & J. R. King (eds) *Avian Biology*. Vol. 1. New York, Academic Press.
Severzow, N. 1873. Allgemeine Übersicht der aralo-tianschanischen Ornis, in ihrer horizontalen und verticalen Verbreitung. *J. Ornith.* 21: 321–389.
Sharpe, R. B. 1874. Accipitres. *Cat. Birds Brit. Mus.* Vol. 1. London.
— 1884. Zoological nomenclature. *Nature* 30: 256–259, 277–279.
— 1899–1909. *A Hand-List of the Genera and Species of Birds*. 5 Vols. London.
Short, L. L. 1969. Taxonomic aspects of avian hybridization. *Auk* 86: 84–105.
— 1972. Hybridization, taxonomy and avian evolution. *Ann. Missouri Bot. Garden* 59: 447–453.
Sibley, C. G. 1955. Ornithology. Pp. 629–659 *in A Century of Progress in the Natural Sciences 1853–1953*. San Francisco, California Academy of Sciences.
Sibley, C. G. & Monroe, Jr., B. L. 1990. *Distribution and Taxonomy of Birds of the World*. New Haven, Yale Univ. Press.
Simpson, G. G. 1943. Criteria for genera, species, and subspecies in zoology and paleozoology. *Ann. New York Acad. Sci.* 44: 145–178.
— 1951. The species concept. *Syst. Zool.* 5: 285–298.
— 1961. *Principles of Animal Taxonomy*. New York, Columbia Univ. Press.
Sloan, P. R. 1979. Buffon, German biology, and the historical interpretation of biological species. *Brit. J. Hist. Sci.* 12: 109–153.
Snow, D. W. (ed.) 1978. *An Atlas of Speciation in African Non-Passerine Birds*. British Museum (Nat. Hist.). London.
Stegmann, B. 1934. Ueber die systematische Stellung von *Phylloscopus lorenzii* (Lorenz). *Orn. Monatsber.* 42: 76–77.
— 1935. Unterschiede im oekologischen Verhalten als taxonomisches Kriterium. *Orn. Monatsber.* 43: 17–20.
Stejneger, L. 1884. On the use of trinomials in American ornithology. *Proc. U.S. Nat. Mus.* 7: 70–80.
Stepanyan, L. S. 1974. [*Inventory and Distribution of Birds of the USSR.*] *Non-Passeriformes*. Moscow. (In Russian.)
— 1978. [*Inventory and Distribution of Birds of the USSR.*] *Passeriformes*. Moscow. (In Russian.)
Sterling, K. B. 1988. Three 19th-century American ornithologists—J. A. Allen, Elliott Coues and C. Hart Merriam—and their leadership in related fields. *Acta XIX Congr. Intern. Orn. (Ottawa 1986)*. Vol. 2: 2724–2736.
Stone, W. 1903. The significance of trinomials. *Condor* 5: 43–45.
— 1935. Some aspects of the subspecies question. *Auk*. 52: 31–39.
Stresemann, E. 1913. Die Vögel von Bali. *Novit. Zool.* 20: 325–387.
— 1919a. Über die europäischen Baumläufer. *Verhandl. Orn. Ges. Bayern* 14: 39–74.
— 1919b. Zur Frage der Entstehung neuer Arten durch Kreuzung. *Cl. Nederl. Vogelkd. Jaarber.* 9: 24–32.
— 1919c. *Sitta europaea homeyeri*: eine reine Rasse oder eine Mischrasse? *Verhandl. Orn. Ges. Bayern* 14: 139–147.
— 1920. Die taxonomische Bedeutung qualitativer Merkmale. *Orn. Beob.* 17: 149–152.

Stresemann, E. 1926. Uebersicht über die "Mutationsstudien" I–XXVI und ihre wichtigsten Ergebnisse. *J. Ornith.* 74: 377–385.

— 1927. Die Entwickelung der Begriffe Art, Varietät, Unterart in der Ornithologie. *Mitt. Ver. Sächs. Ornith.* 2: 1–8.

— 1936. The Formenkreis-Theory. *Auk* 53: 150–158.

— 1943. Ökologische Sippen-, Rassen- und Artunterschiede bei Vögeln. *J. Ornith.* 91: 305–324.

— 1951. *Die Entwicklung der Ornithologie von Aristoteles bis zur Gegenwart.* Berlin, Peters.

— 1962. Leben und Werk von Peter Simon Pallas. *Quellen und Studien zur Geschichte Osteuropas* 12: 247–257.

— 1975. *Ornithology from Aristotle to the Present.* Cambridge, Mass., Harvard Univ. Press.

Strickland, H. E. 1845. Report on the recent progress and present state of ornithology. *Report of the 14th Ann. Meeting of the Brit. Assoc. Adv. Sci. (1844)*: 170–221.

Sudhaus, W. 1984. Artbegriff und Artbildung in zoologischer Sicht. *Z. Zool. Syst. Evol. Forsch.* 22: 183–211.

Sulloway, F. J. 1982a. Darwin's conversion: The Beagle voyage and its aftermath. *J. Hist. Biol.* 15: 325–396.

— 1982b. Darwin and his finches: The evolution of a legend. *J. Hist. Biol.* 15: 1–53.

Sundevall, C. J. 1840. Anteckningar till Skandinaviens Ornithologi. *Kungliga Svenska Vetenskaps-akademien Handlingar*: 31–61.

Swarth, H. S. 1931. The tyranny of the trinomial. *Condor* 33: 160–162.

Sylvester-Bradley, P. C. (ed.). 1956. *The Species Concept in Palaeontology.* The Systematics Assoc. Publ. 2. London.

Szalay, F. S. & Bock, W. J. 1991. Evolutionary theory and systematics: relationships between process and patterns. *Z. Zool. Syst. Evol. Forsch.* 29: 1–39.

Taczanowski, L. 1891–1893. Faune ornithologique de la Sibérie orientale. *Mem. Acad. Wiss. St Petersburg* (7th ser.), vol. 39, part 1 (1891) and part 2 (1893).

Taverner, P. A. 1919. The test of the subspecies. *J. Mammalogy* 1: 124–127.

Thorpe, R. S. 1984. Primary and secondary transition zones in speciation and population differentiation: A phylogenetic analysis of range expansion. *Evolution* 38: 233–243.

Toxopeus, L. J. 1930. *De Soort als Functie van Plaats en Tijd.* Amsterdam, H. J. Paris.

Tristram, H. B. 1859. On the ornithology of northern Africa. Part III. *Ibis* 1: 415–435.

Tschusi zu Schmidhoffen, V. von. 1890. Ueber den Begriff Species und Subspecies in der Ornithologie. *Orn. Jahrbuch* 1: 185–190.

Udvardy, M. von. 1992. Historisches über die geographische Trennung von Populationen durch die pleistozäne Vereisung von Eurasien. *J. Ornith.* (in press).

Vuilleumier, F. 1976. La notion d'espèce en ornithologie. *In Les Problèmes de l'Espèce dans le Règne Animal*, Vol. 1: 29–65. Soc. Zool. France. Paris.

— 1985. Forest birds of Patagonia: ecological geography, speciation, endemism, and faunal history. *Orn. Monogr.* 36: 255–304.

Vuilleumier, F. & Mayr, E. 1987. New species of birds described from 1976 to 1980. *J. Ornith.* 128: 137–150.

Wallace, A. R. 1858. Note on the theory of permanent and geographical varieties. *The Zoologist* 16: 5887–5888.

Wied, Max Prinz von. 1858. Verzeichnis der Vögel, welche auf einer Reise in Nord-America beobachtet wurden. *J. Ornith.* 6: 1–41, 97–124.

Wiglesworth, L. 1898. On formulae for indicating the variation of a species within itself. *Abhandl. Ber. Zool. Anthropol. Mus. Dresden* VII (2): 32–33.

Wiley, E. O. 1981. *Phylogenetics. The Theory and Practice of Phylogenetic Systematics.* New York, Wiley.

Willmann, R. 1983. Biospecies und phylogenetische Systematik. *Z. Zool. Syst. Evol. Forsch.* 21: 241–249.

— 1985. *Die Art in Raum und Zeit.* Hamburg, Parey.

— 1986. Reproductive isolation and the limits of species in time. *Cladistics* 2: 356–358.

Zander, H. D. F. 1851. Einiges über die Abänderungen der *Motacilla alba*, L. und des *Budytes flavus*, Cuv. *Naumannia* 1: 9–21.

Zirnstein, G. 1981. Die Erforschung und Bewertung der Lebenserscheinung "Variabilität" in der Biologie vor 1859. *NTM-Schriftenr. Gesch. Naturwiss., Technik, Med.* 18: 58–78.

Address: Dr J. Haffer, Tommesweg 60, D-4300 Essen-1, Germany.

© British Ornithologists' Club 1992

Systematics and the analysis of integumental lipids: the uropygial gland

by J. Jacob

Received 13 March 1992

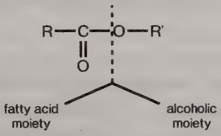
Whilst classification of birds has been exclusively deduced from anatomical, morphological and ethological criteria up to the middle of this century, more recently it became obvious that chemical data also may be used to study the relationships between species. Since DNA codes for all genetically dependent properties, its precise analysis could give us the best answer to questions on classification. Attempts have been made accordingly to use DNA analysis for this purpose, although the method suffers from the fact that no definite structures can presently be obtained, since only the extent of more or less identical sequences may be calculated from the data generated. Nevertheless, Sibley and co-workers have suggested an avian system based upon the so-called DNA/DNA-hybridization experiments (Sibley & Ahlquist 1990).

Since DNA, of course, generally codes for the entire chemistry coursing in the organism which depends on the enzymatic equipment, the analysis of the enzymatic activities being responsible for these processes could also be used for chemotaxonomic attempts (protein patterning). Before DNA hybridization techniques became available, protein patterning had been used in this way by various authors (e.g. Sibley 1970, Sibley & Ahlquist 1972).

Proteins are the final determinant of the formation of the various endogenous as well as the externally released secretions. These secondary metabolites also reflect the enzyme equipment of organisms to a certain extent, although chemotaxonomists using this method must be aware that they are looking through a necessarily small window into the complex reality of life.

The pattern of the lipid constituents formed in the uropygial gland (preen gland) of birds has been found to be very characteristic for a species and fortunately differs markedly between various taxa (Jacob 1978, Jacob & Ziswiler 1982). This has led to a broader investigation of these lipids which may contribute to our understanding of relationships among avian species. Some of these results along with some hitherto unpublished data are reviewed here.

It has been found that preen gland secretions, being the main sources of avian integumental lipids in most instances, consist of monoester waxes, which are composed of a fatty acid and a monohydric alcoholic moiety. The structure may be condensed to the formula:



$$R{-}\underset{\overset{\|}{O}}{C}{-}O{-}R'$$

with R and R′ standing for an alkyl chain $-C_nH_{2n+1}$.

Only few exceptions to this finding have been reported. For instance, in galliform and apterygiform species diols have been found instead of monohydric alcohols. Occasionally also, fatty acids may be replaced by hydroxy acids, as found e.g. in the case of pigeons and in some Ciconiiform species (*Ciconia ciconia*—Jacob 1976, *C. nigra*—Jacob, unpubl.).

Uropygial lipids in systematics

Meanwhile some 500 different species have been analyzed for the chemical composition of their uropygial lipids and a broad structural variety of the above waxes has been detected. Both of the wax moieties may vary in 4 respects:

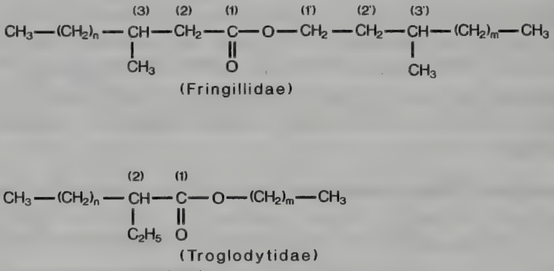
(1) *variation of the chain length*; i.e. 'n' in the above $-C_nH_{2n+1}$ may stand for odd and even numbers from about 6 up to 30;

(2) *variation of the location of the substituent*; i.e. substituents may be located at various carbon atoms. Biochemically there are more basic differences between 2 waxes, one being branched at even and the other at odd carbon atoms compared to 2 waxes both branched at 2 different but even carbon atoms;

(3) *variation of the degree of substitution*; i.e. R and R′ may be more or less alkyl-branched resulting in mono, di-, tri-, tetra- or even penta-methyl-branched acidic and/or alcoholic moieties (e.g. in *Alcedo atthis*);

(4) *variation of the substituent*; i.e. the substituent may be a methyl- ($-CH_3$), an ethyl- ($-C_2H_5$), a propyl- ($-C_3H_7$) or a butyl-group ($-C_4H_9$).

As an example, monoester waxes composed of 3-methyl-substituted fatty acids and 3-methyalkanols have been found as main constituents of the preen wax from finches (Fringillidae), whereas 2-ethyl-substituted fatty acids and unbranched alcohols are structural elements in the case of wrens (Troglodytidae) (Fig. 1.)



$$CH_3-(CH_2)_n-\underset{\displaystyle CH_3}{\overset{(3)}{CH}}-\overset{(2)}{CH_2}-\underset{\displaystyle \overset{\|}{O}}{\overset{(1)}{C}}-O-\overset{(1')}{CH_2}-\overset{(2')}{CH_2}-\underset{\displaystyle CH_3}{\overset{(3')}{CH}}-(CH_2)_m-CH_3$$

(Fringillidae)

$$CH_3-(CH_2)_n-\underset{\displaystyle C_2H_5}{\overset{(2)}{CH}}-\underset{\displaystyle \overset{\|}{O}}{\overset{(1)}{C}}-O-(CH_2)_m-CH_3$$

(Troglodytidae)

n and m = odd- or even-numbered

Figure 1. Examples of different structures of monoester waxes found in finches and in wrens.

Because of the obviously unlimited combination of these structural moieties, an immense number of different final structures may be expected, most if not all of which are actually realized in nature. From this it would not be surprising if each bird had its own specific wax pattern.

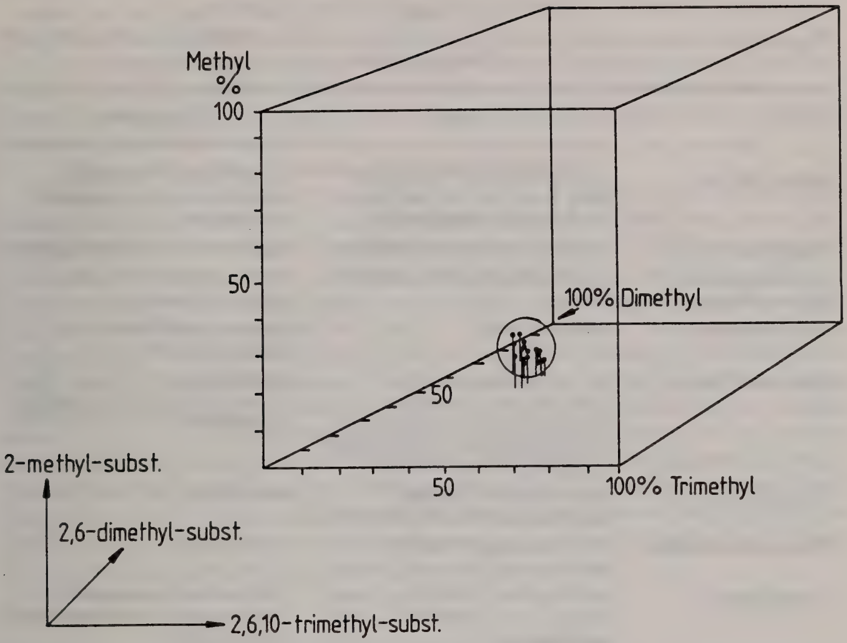


Figure 2. Intraspecific variation of the quantitative composition of wax acids from the uropygial gland secretion of the Blackbird *Turdus merula* (n = 18).

As we know now, however, this is definitely not the case. Prior to chemotaxonomic considerations, the intraspecific variation of the lipid composition has to be checked. This has been done for a number of species and the variation is found to be very limited, as may be seen from Fig. 2, with *Turdus merula* as as example. The circle surrounding the cloud of single points in this figure may be taken as a measure of the degree of intraspecific variation and it is the size of this cloud which decides whether 2 species can be separated by this method. Individuals of a species and its subspecies or races cannot be distinguished from each other by this method. Within different genera, only quantitative differences are found, which in many cases, however, are not significant and hence often cannot be used for classification. *Qualitative* structural differences may be expected at the family level, where at least quantitatively different patterns are observed. Orders may be distinguished by their qualitatively different patterns.

In Table 1 the specific characters for a number of orders are summarized. These data not only allow distinction between orders, but also seem to indicate relationships between some of them. For instance, it appears reasonable to assume that kiwis (Struthioniformes), tinamous (Tinamiformes) and galliform birds (Galliformes) form a group of related orders on the basis of the occurrence of alkane-2,3-diols in all of them. Similarly, Phoenicopteriformes and Anseriformes have many typical

TABLE 1

Typical structural characters found in the uropygial gland waxes in species from different Orders of birds

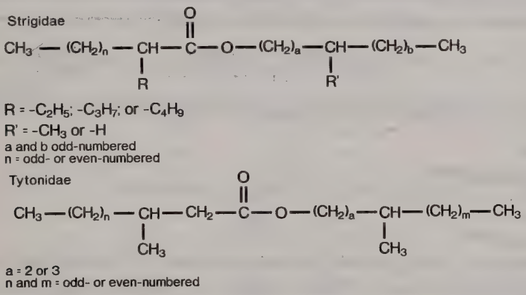
Order	Acid	Alcohols
Sphenisciformes	complex mixture of 2-; 3-; 4-; 2,x-; 3,x-; 4,x-; 2,x,y-; 3,x,y-methyl-substituted acids	2-; 3-; 4-; 2,x-; 3,x-; 4,x-; 2,x,y-; 3,x,y-; 4,x,y,-methyl-substituted
Procellariiformes	similar to the Sphenisciformes	similar to the Sphenisciformes
Struthioniformes (Apterygiformes)	unbranched and 3-hydroxy acids	unbranched alkanols and alkane-2,3-diols
Tinamiformes	unbranched	unbranched alkanols and alkane-2,3-diols
Podicipediformes	3-; 2,x-; 3,x-; 2,x,y-; 3,x,y-; 2,x,y,z-; 3,x,y,z-methyl-substituted as well as 2-ethyl-; 2-ethyl-x-methyl- and 2-ethyl-x,y-dimethyl-substituted	unbranched, 2-; 4-; 2,x-; 4,x-; 2,x,y-; 4,x,y-; 2,x,y,z-methyl-substituted
Ciconiiformes	heterogenous, varying significantly between families	see acids
Phoenicopteriformes	2,6-; 4,6-; 2,x,y-methyl-substituted	unbranched
Anseriformes	unbranched, 2-; 4-; 2,x-; 4,x-; 2,x,y-; 2,x,y,z-methyl-substituted	unbranched; monomethyl-substituted at even-numbered carbon atoms
Falconiformes	2-; 2,x-; 2,x,y-methyl-substituted with the last substituent near the end of the molecule	unbranched; monomethyl-substituted at even-numbered carbon atoms
Gruiformes	2-; 4-; 2,x-; 4,x; 2,x,y; 4,x,y; 2,x,y,z- and 4,x,y,z-methyl-substituted with substituents located at every 4th carbon atom	mainly unsubstituted, otherwise monomethyl-substituted at even-numbered carbon atoms
Charadriiformes	2-; 4-; 2,x-; 4,x-; 2,x,y-methyl-substituted	mainly unsubstituted, otherwise monomethyl-substituted at even-numbered carbon atoms
Galliformes	unsubstituted	alkane-2,3-diols
Columbiformes	unbranched and 3-hydroxy acids	unsubstituted
Psittaciformes	unbranched, 2-, (w-1)- and (w-2)-methyl-substituted	mainly unsubstituted
Cuculiformes	mainly 3-methyl-substituted	mainly 3-methyl-substituted
Strigiformes	2-ethyl, 2-propyl- and 2-butyl-substituted	unbranched and monoethyl-substituted at even-numbered carbon atoms
Apodiformes	3-methyl-substituted	unbranched; 2- and 2,x-methyl-substituted
Piciformes	3-; 3,x-methyl-substituted	unbranched and 3-methyl-substituted
Passeriformes	heterogenous, varying significantly at the family level	see acids

constituents in common, and this holds also for the Sphenisciformes and the Procellariiformes.

Two examples may be given for the contribution of preen wax analysis to systematic questions: (1) the separation of the Tytonidae (barn owls) from the Strigiformes (owls) and (2) the systematic position of *Vultur gryphus* (the Condor).

Separation of the Tytonidae from the Strigidae

The chemical composition of the uropygial gland waxes of various owls (Jacob & Poltz 1974, Jacob & Hoerschelmann 1984) indicates that Strigiformes are characterized by the occurrence of 2-alkyl-substituted fatty acids with an ethyl-, propyl- and/or a butyl substituent, all very rare compounds, hardly any of which have been found anywhere else in nature. The alcoholic moiety is composed of unbranched and monomethyl-branched alkanols with a methyl substituent located at an even carbon atom. However, *Tyto* possesses an entirely different wax pattern composed of 3-methyl- and 3,x-dimethyl-substituted fatty acids and 3-, 3,x-, 4, and 4,x-methyl-substituted alcohols. Hence, Tytonidae may be readily distinguished from Strigidae by basic differences in their preen wax composition, as can be seen from Fig. 3. The barn owls (if they are owls at all) seem to link the owls with some other Orders such as Piciformes, Cuculiformes and Apodiformes, in which identical or at least very similar structures have been detected.



Strigidae

$$CH_3-(CH_2)_n-\underset{R}{\underset{|}{CH}}-\overset{O}{\overset{\|}{C}}-O-(CH_2)_a-\underset{R'}{\underset{|}{CH}}-(CH_2)_b-CH_3$$

$R = -C_2H_5$; $-C_3H_7$; or $-C_4H_9$
$R' = -CH_3$ or $-H$
a and b odd-numbered
n = odd- or even-numbered

Tytonidae

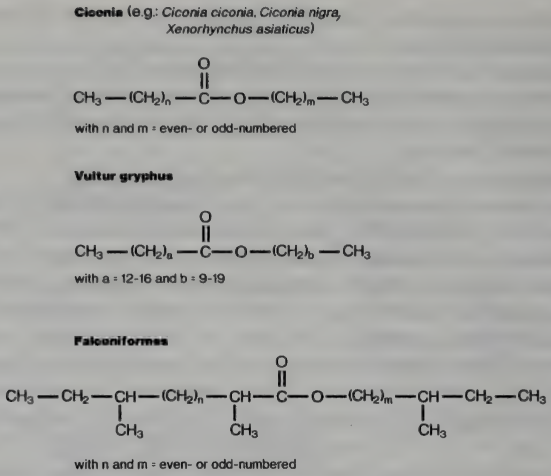
$$CH_3-(CH_2)_n-\underset{CH_3}{\underset{|}{CH}}-CH_2-\overset{O}{\overset{\|}{C}}-O-(CH_2)_a-\underset{CH_3}{\underset{|}{CH}}-(CH_2)_m-CH_3$$

a = 2 or 3
n and m = odd- or even-numbered

Figure 3. Chemical structures found in the preen waxes of Strigidae and Tytonidae.

The systematic position of the Condor Vultur gryphus

A nice example for an interdisciplinary approach to the solution of systematic problems has recently been given by comparing biochemical and ethological findings in the case of the Condor *Vultur gryphus* (Cathartidae). Although Beddard (1898) found similarities between Cathartidae and Ciconiiformes nearly 100 years ago, other biologists have generally associated *Vultur* with the birds of prey rather than with the Ciconiiform birds. König (1982) found support for Beddard's statement by studying the mating behaviour; and as presented in Figure 4, a comparative analysis of the preen wax composition of the Condor, storks and birds of prey clearly shows that identical wax patterns are synthesized in storks and in the Condor (Jacob 1983). These findings have now also been confirmed by DNA/DNA-hybridization experiments (Sibley & Ahlquist 1986).


Ciconia (e.g.: Ciconia ciconia, Ciconia nigra, Xenorhynchus asiaticus)
with n and m = even- or odd-numbered
Vultur gryphus
with a = 12-16 and b = 9-19
Falconiformes
with n and m = even- or odd-numbered

$$CH_3-(CH_2)_n-\overset{\overset{O}{\|}}{C}-O-(CH_2)_m-CH_3$$

$$CH_3-(CH_2)_a-\overset{\overset{O}{\|}}{C}-O-(CH_2)_b-CH_3$$

$$CH_3-CH_2-\underset{CH_3}{\underset{|}{CH}}-(CH_2)_n-\underset{CH_3}{\underset{|}{CH}}-\overset{\overset{O}{\|}}{C}-O-(CH_2)_m-\underset{CH_3}{\underset{|}{CH}}-CH_2-CH_3$$

Figure 4. Chemical structures found in the preen waxes of *Vultur gryphus*, Ciconiiformes and Falconiformes.

TABLE 2
Preen wax types found in the uropygial gland of Ciconiiform birds

	Monoester waxes* type I	type II	type III	Diester waxes	Triglycerides
Ciconia ciconia	+	−	−	+	+
*Ciconia nigra****	+	−	−	+	+
*Xenorhynchus asiaticus****	+	−	−	−	−
*Egretta alba****	+	+	−	−	−
*Egretta sacra****	+	+	−	−	−
*Platalea leucorodia****	+	+	−	−	−
Scopus umbretta	+	+	−	−	−
Theristicus caudatus	(+)	+	−	−	−
Threskiornis aethiopicus	−	+	−	−	−
Ardea cinerea	+	−	−	−	+
*Ardea novaehollandiae****	+	+	+	−	−
Nycticorax nycticorax	+	−	+	−	−
*Botaurus poiciloptilus****	−	+	+	−	−
*Leptoptilos crumeniferus***	−	−	−	−	+

*type I: unbranched acids containing monoester waxes; type II; branched acids containing monoester waxes; type III: secondary alcohols containing monoester waxes
**feather lipids
***unpublished data

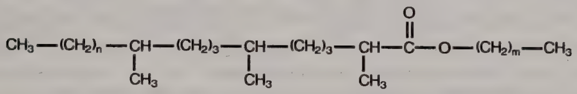
Ciconiiformes

In almost all Orders so far investigated, specific structures have been found so that species may be attributed to these taxa. There is, however, a remarkable exception to this in the case of the Ciconiiformes, where the composition of the waxes broadly varies. Not only the wax moieties but also the total lipid composition itself differs among the various families, in that monoester waxes are found in *Egretta, Threskiornis, Theristicus, Platalea* and *Scopus*, whereas additional diester waxes and triglycerides are detected in *Ciconia*. In Ciconiiformes also species exist which possess secondary alcohols as one wax moiety (*Botaurus, Nycticorax, Ardea*). The findings summarized in Table 2 may indicate a polyphyletic origin for the order Ciconiiformes.

Passeriformes

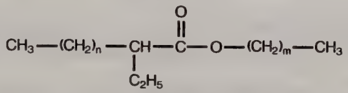
From a chemotaxonomic viewpoint, the hitherto investigated species of the large order Passeriformes may be separated into at least 4 chemical groups according to their preen wax types:

(1) waxes composed of unbranched alcohols and more or less highly methyl-branched acids substituted at every 4th carbon atom, with the first branch located at the 2- or 4-position.
The following families or subfamilies may be attributed to this group: the Tyrannidae, Funariidae of the Suboscines, and also the Corvidae, Alaudidae, Bombycillidae, Oriolidae, Monarchidae, Timaliinae, Pachycephalinae, Hirundinidae of the Oscines.



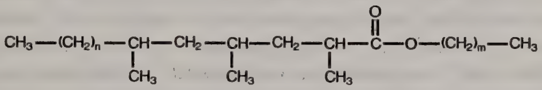
$$CH_3-(CH_2)_n-\underset{CH_3}{\underset{|}{CH}}-(CH_2)_3-\underset{CH_3}{\underset{|}{CH}}-(CH_2)_3-\underset{CH_3}{\underset{|}{CH}}-\overset{O}{\overset{\|}{C}}-O-(CH_2)_m-CH_3$$

(2) waxes composed of unbranched alcohols and 2-ethyl-substituted fatty acids.
The Paridae and Troglodytidae may be combined in this group.



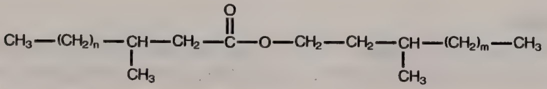
$$CH_3-(CH_2)_n-\underset{C_2H_5}{\underset{|}{CH}}-\overset{O}{\overset{\|}{C}}-O-(CH_2)_m-CH_3$$

(3) waxes composed of unbranched alcohols and more or less highly branched fatty acids in which every 2nd carbon atom bears a methyl group, the first of which is located at carbon atom 2.
The Ploceidae and Estrildidae are found in this group.



$$CH_3-(CH_2)_n-\underset{CH_3}{\underset{|}{CH}}-CH_2-\underset{CH_3}{\underset{|}{CH}}-CH_2-\underset{CH_3}{\underset{|}{CH}}-\overset{O}{\overset{\|}{C}}-O-(CH_2)_m-CH_3$$

(4) waxes composed of 3-methylsubstituted alcohols and 3-methyl-substituted fatty acids.
To this group may be attributed the Fringillidae, Emberizidae, Passerinae, Motacillidae, Icteridae, Prunellidae, Carduelidae, Thraupidae.

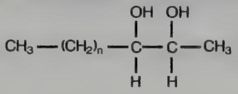


$$CH_3-(CH_2)_n-\underset{CH_3}{\underset{|}{CH}}-CH_2-\overset{O}{\overset{\|}{C}}-O-CH_2-CH_2-\underset{CH_3}{\underset{|}{CH}}-(CH_2)_m-CH_3$$

General considerations

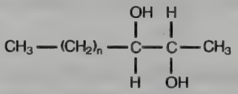
Generally speaking, there are Orders which are characterized by a very broad spectrum of different lipid constituents and others in which highly specific structures are found. Very complex mixtures occur in Sphenisciformes, Procellariiformes and Podicipediformes. A smaller complex of different acids and alcohols are found in Gruiformes, Falconiformes, Strigiformes, Psittaciformes, Anseriformes and Phoenicopteriformes. In Galliformes, Coraciiformes, Cuculiformes, Piciformes and various Passeriformes the structural variation is even more restricted inasmuch as mostly only one homologous series of acids or alcohols participates in the spectrum of the preen wax. Extremely simple wax structures composed of only *one* acid and *one* alcohol have been detected in *Cinclus cinclus* (Bertelsen *et al.* 1975) and in many weaver-birds (e.g. in *Ploceus cucullatus, P. subaureus, P. galbula*—Poltz & Jacob 1973) indicating the presence of a highly specific enzyme system in these species.

Since weaver-birds are considered to be more recent steps in avian evolution, it appears that preen wax patterns become more specific and less complex with progressing speciation—a trend which has also been observed for the cuticular lipids of beetles (Jacob & Hanssen 1985). Under the assumption that this is a general principle, an interesting conclusion may be drawn for the order Galliformes. The preen waxes of species from this order are characterized by the occurrence of alkane-2,3-diols for which 2 stereoisomeric forms are known (*threo*- and *erythro*-)



$$CH_3—(CH_2)_n—\underset{H}{\overset{OH}{C}}—\underset{H}{\overset{OH}{C}}—CH_3$$

erythro form



$$CH_3—(CH_2)_n—\underset{H}{\overset{OH}{C}}—\underset{OH}{\overset{H}{C}}—CH_3$$

threo form

(with n = even- or odd-numbered

Mixtures of both forms have been found in *Gallus* and *Coturnix*, whereas *Leipoa, Meleagris* and *Perdix* possess only the *erythro*-forms. By contrast, *Phasianus colchicus* produces only one single diol, namely the *erythro*-octadecane-2,3-diol, i.e. a high stereo- and chain-length-specificity of the synthesizing enzyme(s) is expressed in this species. Following the hypothesis of a progressing chemical specialization, *Gallus* and *Coturnix* ought to be considered as ancient, *Leipoa, Meleagris* and *Perdix* as more recent forms and *Phasianus* as a preliminary endpoint of the evolution of the Galliformes. Within the closely related species *Gallus* and *Phasianus* and the couple *Coturnix* and *Perdix*, in both cases the second named are obviously the more modern forms.

Conclusions

Summarizing the results of preen gland analysis obtained from about 500 different species it seems that the wax composition is a helpful parameter for avian systematics. The slogan "Show me your preen gland secretion and I shall tell you who you are" certainly exaggerates and overestimates the significance of this character. Preen wax analysis, however, has contributed to the solution of several systematic questions and the data should be treated as one piece of a very complex puzzle.

References:
Beddard, F. E. 1898. *The Structure and Classification of Birds*. Longmans, Green, London.
Bertelsen, O., Eliasson, B., Odham, G. & Stenhagen, E. 1975. The chemical composition of the free-flowing secretion of the preen gland of the Dipper (*Cinclus cinclus*). *Chem. Scr.* 8: 5–7.
Jacob, J. 1976. Diester waxes containing 2-hydroxy fatty acids from the uropygial gland secretion of the White Stork (*Ciconia ciconia*). *Lipids* 11: 816–818.
— 1978. Uropygial gland secretions and feather waxes. Pp. 165–211 *in* A. H. Brush (ed.), *Chemical Zoology*, Vol. X.
— 1983. Zur systematischen Stellung von *Vultur gryphus* (Cathartiformes). *J. Orn.* 124: 83–86.
Jacob, J. & Hanssen, H.-P. 1985. Distribution and variability of cuticular hydrocarbons within the coleoptera. *Biochem. Syst. Ecol.* 14: 207–210.
Jacob, J. & Hoerschelmann, H. 1984. Chemotaxonomische Untersuchungen an Eulen (Strigiformes). *Funkt. Biol. Med.* 3: 56–61.
Jacob, J. & Poltz, J. 1974. Chemical composition of the uropygial gland secretions of owls. *J. Lipid Res.* 15: 243–248.
Jacob, J. & Ziswiler, V. 1982. The uropygial gland. Pp. 199–324 *in* D. S. Farner, J. R. King & K. C. Parkes (eds.), *Avian Biology*, Vol. VI. Academic Press, New York.
König, C. 1982. Zur systematischen Stellung der Neuweltgeier (Cathartidae). *J. Orn.* 123: 259–267.
Poltz, J. & Jacob, J. 1973. Bürzeldrüsensekrete von Webervögeln (Ploceidae). *Z. Naturforsch.* 28c: 449–452.
Sibley, C. G. 1970. A comparative study of the egg-white protein of passerine birds. Peabody Museum of Natural History. *Yale University, New Haven. Bull.* 32.
Sibley, C. G. & Ahlquist, J. E. 1972. A comparative study of the egg-white protein of non-passerine birds. Peabody Museum of Natural History. *Yale University, New Haven. Bull.* 39.
—, — 1986. Der DNA-Stammbaum der Vögel. *Spektr. Wissenschaft* (5/86): 96–107.
—, — 1990. *Phylogeny and Classification of Birds*. 976 pp. Yale University Press. New Haven & London.

Address: Dr Jürgen Jacob, University of Hamburg, Zoological Institute and Zoological Museum, Martin-Luther-King-Platz 3, D-2000 Hamburg 13, Germany.

© British Ornithologists' Club 1992

Under the skin: the bird collections of the Natural History Museum

by Alan G. Knox & Michael Walters

Received 28 April 1992

BRN 289033

The bird collections of the Natural History Museum (NHM), formerly known as the British Museum (Natural History) or BMNH, have been housed at Tring, in Hertfordshire since the early 1970s. Increasing pressure on space at South Kensington in London caused the move out of town, to a site adjacent to the public galleries of the Zoological Museum at Tring. The latter had been bequeathed to the BMNH by Walter, Lord Rothschild, in 1937. The circumstances of the bequest, and the earlier sale of most of Rothschild's bird skins to the American Museum of Natural History, are described by Murphy (no date) and Rothschild (1983). The Tring public galleries are still maintained as a splendid example of a Victorian natural history museum, undoubtedly the finest in the country, devoted entirely to the spectacle of diversity. Some of the best taxidermy of the period is on display.

This paper describes briefly the museum at Tring, outlines the scope and nature of the NHM bird collections and presents information about the specimens and their documentation. Attention is drawn to some of the possible sources of inaccuracy associated with museum data. Some of this information is relevant to any large collection. The curatorial comments may be of interest to staff with responsibilities for bird collections in other museums.

The NHM holds over one million bird skins, one million eggs, 13,000 anatomical specimens and 8000 skeletons, making it one of the 2 largest bird collections in the world. It is particularly rich in historic material and types.

THE TRING BUILDINGS AND FACILITIES

The Tring site consists of 2 main buildings linked together. The older part contains the Rothschild public galleries, with offices, stores and part of the library behind and below. On the other side of the car-park is the purpose-built, 4-storey, air-conditioned block which houses most of the bird collections. Between these lies a single-storey building with security/reception, offices, packing room, walk-in freezer, laboratory, staff room and a connecting corridor to join the main buildings together. Behind this block sits another large walk-in freezer and the separate dermestarium with a chemical store attached. The dermestarium consists of 2 rooms: an office/preparation area and the environmentally-controlled beetle colony where *Dermestes* beetles are used to strip carcasses.

For further information on the Museum at Tring, see Clancey (1984).

Libraries

The NHM has the finest natural history library in the world. Most of the holdings are at the main Museum site at South Kensington, in

London, but the bird library is at Tring. It is probably the best bird library in the world concentrating on faunistics and works on taxonomic groups. Historically, the library comprised 2 main parts, the Rothschild Library (part of the bequest) and the library of the NHM bird section. The distinction is now less clear as the holdings have become integrated. At his death Rothschild's library was incomparably complete in the older literature and books on travel, exploration and big game hunting, and is housed in an exquisite 3-level balconied room. This area is not normally open to visitors. The remainder of the library at Tring is currently dispersed in several parts of the buildings. It is not a lending library, but is available to visitors by appointment and enquiries by post. Charges are made for photocopies.

Storage units: the Tring cabinets

Most of the bird skins, as well as the eggs, nests and skeletons are stored in specially constructed cabinets.

These cabinets consist of two 2-door units one on top of the other. Each unit has a removable central divider and may thus take either full- or half-width plastic drawers sliding on plastic runners. The carcasses of the cabinets are constructed from chip-board, which works well with half-width drawers, but has bowed slightly on some cases allowing some full-width drawers to drop. This is easily corrected with small wedges between the cases.

The doors are metal skinned, with refrigerator-type magnetic seals. The plastic skin on the door seals has become tacky on many units, and the adhesive bonding the metal strip to the carcasses has failed in places. Each door has a label holder on the outside and a recessed pocket for insecticide within. The door pockets in the bird skin cabinets contain insecticide, which is changed twice yearly. Until recently ceramic tiles impregnated with DDVP (Dichlorvos) were used, but these have been replaced with commercial Secto units in plastic cases. Severe corrosion is usual around the pockets, and ink from fibre-tipped pens used to label the drawers smudges and becomes illegible near the pockets. Pesticide levels within the cases are said to conform with recommended levels, but there is a strong odour on opening the doors and some users have experienced persistent headaches. Visitors to the collection are recommended to open the cases and allow them to ventilate before working with the specimens. The continued use of DDVP is being reviewed.

Within the half-width drawers many of the specimens are held in heavy, plastic-laminated cardboard trays in 5 modular sizes from 2 to each drawer down to 32.

The skins of many species have been divided into subspecies, and within each subspecies into separate sexes, age classes or by geographic origin as appropriate. The labels of the birds in each group are marked with numbered and coloured gummed paper spots and, for small birds, the groups are put in separate trays. This system has been found to aid research and curation, and helps users to return skins to the correct trays. Trays containing groups of interest may easily be carried to side benches for study.

The use of plastic drawers and laminated trays help to reduce abrasion on the skins and minimize the soiling of feathers which may occur in drawers constructed from less sympathetic materials.

THE BIRD COLLECTIONS

Spirit and skeleton collections

The ground floor of the main (new) building contains the spirit and skeleton specimens. The spirit collection is held in 70% industrial methylated spirit in the usual variety of bottles and jars on metal racking. Glass-topped bottles and jars with ground-glass stoppers are preferred, the most recent ones having been purchased from eastern Europe. Plastic-topped containers are being replaced whenever possible. Most of the larger specimens are contained in plastic buckets with lids, but the

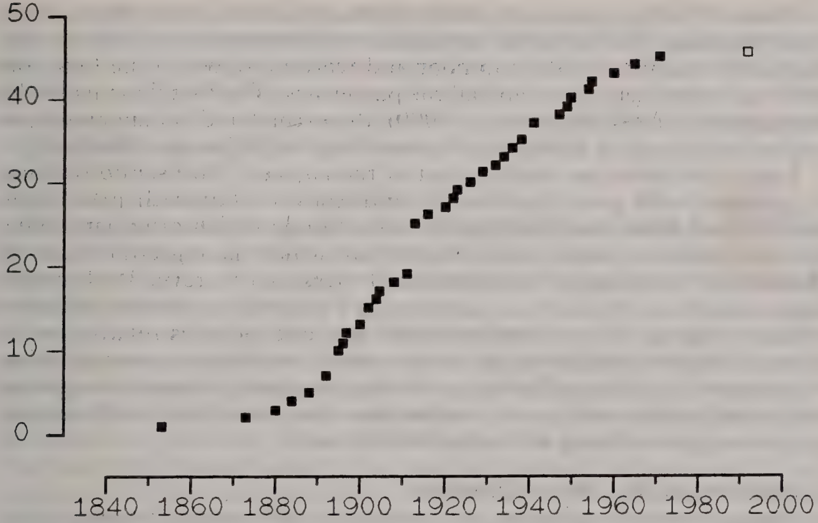


Figure 1. Growth of the Natural History Museum collections. Horizontal axis: year. Vertical axis: number of completed *Aves registers* (including sets of Special Collections *Registers*). The open symbol indicates a volume half-completed in 1992. (The use of the *Registers* in this way gives only an approximation of the growth of the collections.)

buckets occasionally split. The collection is arranged in systematic order following Peters (1931–87), the main exception being a metal cabinet housing extinct birds and historic or otherwise important specimens, including 2 birds collected on Cook's last voyage, one of which is still in its original bottle.

All but the largest skeletons are held in glass-topped boxes with labels clearly visible so that the contents may be checked without the need to open them. Several cabinets are reserved for important material, separate from the main systematic series.

The holdings of the anatomical and skeleton collections have recently been summarised by Blandamer & Burton (1979), Wood & Jenkinson (1984), Wood & Schnell (1986) and Wood *et al*. (1982a, 1982b). There are no skin-skeletons or long series of skeletons of individual species, or special tissue collections for biochemical research.

The skin collection

The large skin collection contains representatives of almost every species and subspecies listed by Peters (1931–87). In terms of numbers of individuals, geographic coverage is best for the Palaearctic, Africa, India and North America, and poorest for South America.

The collection dates mainly from the late 19th and early 20th centuries, and relatively little material has been acquired in the last 40 years (Fig. 1). Only 7 new skins were registered in 1986, and fewer than 50 per year is now usual.

Most of the bird skins are on the first, second and third floors of the main building. The birds are arranged in systematic order with the non-passerines starting on the top floor and working down to the first floor with the 'near-passerines' and all the passerines. The first floor also holds segregated series of the types (*c.* 8000), the extinct and endangered birds and a few historic or delicate collections (e.g. the Montagu collection).

Large bird skins are held in part of the adjacent Rothschild building in cabinets with good frameworks and drawers, but with poor fronts constructed from modified plastic roller-blinds which often jam. They are also neither insect- nor dust-proof which is regrettable as the Rothschild building is environmentally less satisfactory. Rothschild's large collection of mounted cassowaries *Casuarius* haunt the basement of this building in even poorer conditions, but 'poor' is relative in this context. Most museums would envy even the worst store-room at Tring.

A separate building (the Annex) in the same street is used as a general store and houses the Museum's collection of mounted birds without data, many on open shelving with roller-blind fronts.

Condition of the skin collection

Being a very old collection, with relatively little recent material, many of the skins are not in the best of condition. Amongst the large birds in particular, damage from grease is common. The smaller birds suffer more often from detached legs, wings and heads, and this is worst in frequently-used groups such as the *Phylloscopus* warblers. Detached labels can occur anywhere in the collection, often the result of grease damage and/or embrittlement of the paper or poor handling or both. These problems will get worse rather than better as the collection grows still older and is used more, highlighting the conflict between use and conservation. Indeed, the oldest and most historically important specimens are amongst those at greatest risk. The need for adequate conservation resources is a problem in most bird skin collections throughout the world and, until it is addressed properly, irreplaceable specimens will continue to be threatened.

Documentation

There is no card- or other index to the whole collection, indeed only the extinct and endangered birds have been entered onto computer (Knox & Walters, MS). Apart from the information on the labels, field-notes that may have been lodged in the library and anything that may have been published about individual specimens, the only documentation to the collection is the *Registers* or the old *Catalogues* (see below). The monumental, 27 volume, *Catalogue of Birds in the British Museum*, published between 1874 and 1898 (Sharpe and others 1874–98), contains some details of the specimens in the collections at the time each group was revised. This work frequently reveals information on extant specimens that is not on the labels, and indicates where other specimens have since disappeared to or have been reidentified.

THE INFORMATION ASSOCIATED WITH THE BIRD SKINS

The quality of data associated with specimens in many museums, particularly the older specimens, is extremely poor and often contradictory.

This problem has been discussed previously by e.g. Van Tyne (1952), Clench (1976), Conover & Hunt (1989) and Parkes (1989a,b). Recommendations for critical data have recently been made by Foster & Cannell (1990). In the following section, although we discuss the quality of the data with particular reference to the collections of the NHM, many points apply equally to any large collection.

Museum registration numbers

Many specimens, skins in particular—perhaps as many as 100,000—have never been registered. In other cases, specimens were dealt with in blocks—for instance, a large part of the great Shelley collection occupies only 7 lines in the register.

Attempts to check numbers on labels against the original register entries reveals many irregularities. Some numbers were written incorrectly on the labels (or even in the register): given time, most, but not all, of these may be traced. Duplicate numbers are sometimes encountered. Many arise from the Special Collections registers (see below), but for others it is clear that 2 or more specimens (usually, but not always, with the same data) were registered with the same number without this information being noted in the register. Details of the *Registers* and *Catalogues* of the collection are given below.

Locality data on labels

Tracing place-names is often a difficult task, particularly with older museum specimens. The handwriting on labels is frequently illegible or nearly so, and may be in a foreign language or a collector's shorthand. Local names which do not appear on maps or in gazetteers are regularly encountered. Much collecting took place before detailed maps of the relevant countries had been prepared, and at a time before place-names had ever been written down. It was not unknown for a collector to use several different spellings for the same place-name, or different names for the same place. Some common place-names can be found repeatedly within a single country and in some countries place-names change with the political climate. Chinese place-names have their own special problems, as do many from the Near East.

Two other significant practices serve to introduce uncertainty concerning many of the apparent localities of older specimens. The first relates to localities not noted at the time of collection, the second, to the widespread removal of original labels.

The importance of precise locality (or any other) information was not recognised by many early collectors; large numbers of specimens bear no data at all or, at best, a country or continent alone. Other collectors made up labels long after the specimens were obtained, with the attendant possibility of errors of memory or transcription. A few unscrupulous collectors or dealers fabricated data to enhance the monetary or scientific value of their specimens (e.g. see Nicholson & Ferguson-Lees 1962). The huge Meinertzhagen collection at the NHM has many skins bearing incorrect data, including a number taken from the then BMNH and subsequently relabelled (for the evidence see Clancey 1984, Cocker 1990: 274–5; also A.G.K. pers. obs.).

Specimens were frequently obtained in batches from collectors (often native) and shipped through dealers and transit ports and, at any stage of this process, erroneous data could become associated with the specimens, inadvertently or otherwise. Some dealers (and even museums) attached their own labels, often carrying generalised distribution data relating to the range of the species rather than the locality of the individual. The data were not even safe when the specimens reached the British Museum. For a while, localities and dates were routinely transferred to Museum labels, and all others removed (Sharpe 1906). Many errors arose in this way. The practice was not that of the British Museum alone, but was widespread among curators until the late 19th century. Where additional labels had been attached to specimens and the earlier ones retained, errors of transcription are frequently noted. Examples may be found in Knox & Walters (MS).

Particular care is required when dealing with specimens which are mounts or ex-mounts. For a long time during the 18th and early 19th centuries all important specimens were set up for display in the public galleries of the Museum. Such specimens usually had their labels removed and, with some, the data written on the base of the mount or printed on the accompanying gallery label. Few of the latter still exist and many of the old gallery specimens have since been unmounted and transferred to the general skin collection. Most specimens which were formerly mounted (or are still mounts) lack data; with others there are doubts concerning the veracity of data after repeated transcription. In a few cases it is clear that when gallery specimens became damaged, or better ones became available, birds were substituted without necessarily changing the data. Some were placed on mounts formerly occupied by conspecifics or quite different species. Since the late 1980s, the Museum has not unmounted birds for them to be placed in the general skin collection, as the former practice often led to the loss of information concerning the history of the specimens.

Date of collection, or date of death of specimens from captivity

Many of the comments made above regarding the reliability of locality data apply equally to the date, where the information may have been transcribed several times or added long after collection. At its worst, during the preparation of the *Catalogue of Extinct and Endangered Birds* (Knox & Walters, MS), three different dates (without comment) were found on separate labels attached to a single specimen.

The labels on many specimens, particularly from the Salvin-Godman and Sclater collections, bear dates usually consisting of the year, or the month and year only, written close to the thread holes at the left-hand end. In some cases it appears that these are the dates of collection and in others, that they are the dates when the specimens were received. Where the label bears only one date, it is not possible to tell which it is. Where 2 dates appear, they are sometimes the same but, more usually, the left-hand one is later.

The labels to some older bird skins also bear the dates when the specimens were sent to the 'stuffers', usually to be unmounted, cleaned or repaired. It is only too easy to mistake this for the date of collection, particularly if the latter was not recorded. The stuffer's name (not always given) or a date several decades after the year of registration are the main warnings, but some stuffers' dates are disturbingly plausible as dates of collection. The NHM still holds several volumes of notebooks recording the movements of specimens to and from various stuffers, including Burton, Cullingford, Dodson, Gerrard, Gunn, Pickhardt, Rye and West, for the period 1871–1895.

Information on the original collector (if known), or the route by which the specimen reached the Museum

The names of the original collectors, dealers, private collectors and other intermediaries through whose hands and/or ownership the specimens passed before they came to the Museum have caused almost as many problems as the place-names. Alternative spellings, difficult handwriting, initials without full surnames and other missing or incomplete data pervade the collections and the registers.

For information on many collectors and donors, see Sharpe (1906), Warren & Harrison (1966–73) and Mearns & Mearns (1988).

Age and sex data

Although many or most specimens were probably examined internally at the time of collection, this is rarely noted on the label. A proportion of specimens will have been mis-sexed, for 2 main reasons. Firstly, for some, sex will have been determined on the basis of (incorrectly) presumed plumage or mensural differences, either on collection, or at any time subsequently. Secondly, mistakes may have been made in the internal sexing of specimens that were damaged or partly decayed, or with small sexual organs (particularly during the refractory period). Careful sexing (with notes and sketches of the gonads, and the name of the preparator) is particularly important with skeletal material, in which there is the additional danger of misidentification of species. Fig. 2 illustrates mis-sexing in some skeletal material.

For further discussion on the reliability of sex information on museum labels, see Clench (1976) and Parkes (1989a,b).

Duplicates

Occasional reference will be found on labels or in the literature to 'duplicates'. For a long time (since the late 1700s) it was the practice to select only the best specimens for the NHM's collections, and consign the others to the 'duplicates', in the basement. Very large numbers of birds were so designated. They were kept separately from the main series, and the labels were usually annotated 'duplicate', 'dupl.' or 'dup.'. These birds were often used for exchange or presentation. Storage space was always at a premium when the bird collections were held in London, either at Bloomsbury, or later at South Kensington. From the 1940s until the late 1960s, many drawers were so full that specimens without good data were removed and sent to Tring Zoological Museum, where the 'duplicates' were then housed. Similarly, poor specimens, or ones with incomplete data from newly received collections were dispatched regularly by van to Tring. Although the assignment of new duplicates has

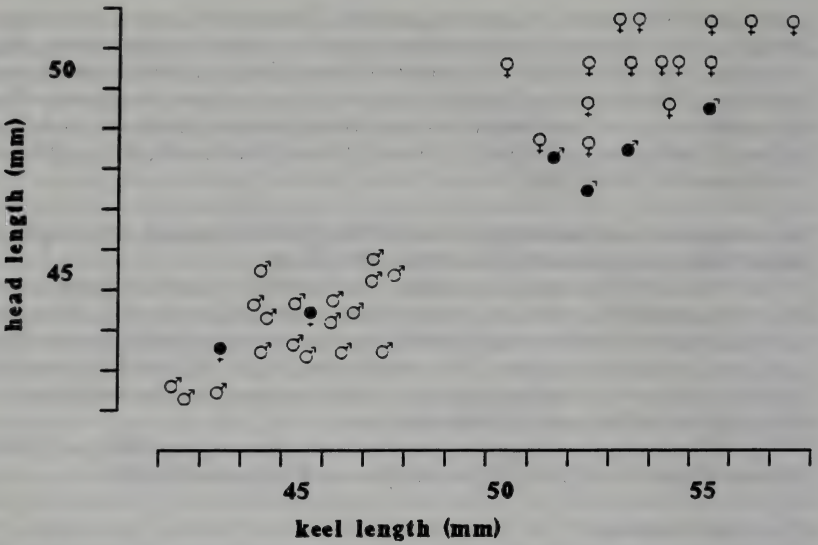


Figure 2. Skeletal measurements of British Sparrowhawks *Accipiter nisus* in the Natural History Museum, registered 1951–1988. Symbols denote sex as shown on the box labels. Filled symbols indicate specimens presumed to have been sexed incorrectly. Most species of birds show less sexual dimorphism in size than the Sparrowhawk and mis-sexing would be more difficult to test in their case.

ceased, it has not yet been possible to reincorporate all the previously separated material, and drawers or trays marked 'duplicates' may still be found in the collection.

Missing specimens

Specimens known or thought to have been in the collections are sometimes unable to be located. Indeed, a significant number of specimens could not be found during a recent NHM cataloguing project (Knox & Walters, MS). Specimens which are listed in the registers, in the *Catalogue of Birds* or elsewhere can appear to go missing for a variety of reasons. Some will have been re-identified and moved to a different part of the collection; some will have been exchanged or given away; a few will even have been so badly damaged by insects or other causes that they have been subsequently destroyed. In all these cases, it would have been usual to annotate the register accordingly, but this sometimes was not done. Furthermore, specimens are not infrequently put back in the wrong place in the collection by visitors (and occasionally by staff): with a collection as large as that of the NHM, it becomes difficult to relocate specimens misplaced in this way. Some genuinely will have been lost, and a few will possibly have been stolen (see e.g. Clancey 1984). A quantity of eggs from the Jourdain collection were never actually received, although the card-index might suggest otherwise. Likewise, some other specimens that the Museum is said to possess, never arrived, and a small number of entries may be clerical errors. Many older labels were made of flimsy paper or card that has become brittle. When the specimens became separated from their labels (as many of them did), they became unrecognizable and, effectively, lost.

The Old Collection

As far as we can ascertain, the term 'Old Collection' has been used in a variety of contexts. It seems to have been applied to the collection which was housed in the public rooms of Montagu House in the early 1800s, at least part of which was then moved to the galleries of the new British Museum (completed on the same site in 1845). Some specimens remained on show until at least the 1870s, but others were removed from time to time and placed in the study collections. 'Old Coll.' appears without definition in the *Catalogue of Birds*, apparently referring to various old, or not so old, usually unregistered, specimens. The term has also been used, seemingly without much discrimination, at various other stages.

Type specimens

Many labels bear the inscription 'type'. Most of these do not refer to name-bearing types, but to specimens that are 'typical' in some way. Holotypes and syntypes identified or selected by Warren & Harrison (1966–73) and others are segregated into separate cabinets and carry red labels for easy identification.

Additional comments

The collection mainly being old, the labels rarely carry information about bare-part coloration, stomach contents and so forth.

THE EGG COLLECTION

Like the skeletons, the egg collection is stored in clearly labelled glass-topped boxes. Within each box the eggs rest in individual depressions in cotton wool, restrained from movement which could damage them during curation or while being studied. The boxes also provide additional protection against atmospheric particulates. For security, the cabinets are locked and unlabelled.

Approximate size of the collection

The egg collection is believed to be the largest in the world. The eggs have never been counted and, because eggs are usually kept and catalogued in sets or clutches of varying size, the number of items catalogued is not an indication of the total size of the collection. (A set is regarded as one or more eggs of the same species collected or received together, not necessarily a clutch.) About half the cabinets in the systematic series have been revised and, by random counts of specimens in the remainder, an estimate of *c.* 1,000,000 eggs has been made. To arrive at an average number of clutches it might be necessary to divide this total by 3–4.

The age of the specimens

Only a few of the Museum's eggs are more than 150 years old. The earliest so far found is of a Northern Gannet *Morus bassanus* from the Bass Rock, in Scotland, collected in 1807. It is probable that some undated eggs are older than this. A number are labelled 'Old Collection', and among them are probably the ones referred to by Lankester and by Oates on pp. v and vii of Oates (1901). These were from a very early collection displayed in the public galleries. Many of the eggs listed in the main text of Oates (1901–12) as being from the Old Collection were more recent, having been acquired from nineteenth century dealers such as Fraser, Warwick and Parzudaki, though they share with the old eggs the lack of data and dates. There are also a number of eggs listed as 'Montagu collection' or 'ex Montagu Museum'. These were probably received at the same time as the Montagu collection of bird skins (1816) and some may be of eighteenth century vintage.

Most of the Museum collection (about 90–95%) dates from the latter half of the nineteenth century and early part of the twentieth. Apart from the Pitman and Benson east African collections, and more recent confiscations of eggs taken illegally in this country, there is little material from later than about 1940.

Systematic coverage

The eggs are stored and curated in systematic order, following Peters (1931–87). There are specimens from all orders and nearly all families, apart from a few which are monotypic. The nests and eggs of about one third to one quarter of the world's species may still be undiscovered or undescribed; in addition, a number of species from remote areas are not represented. Nevertheless, this is probably the most comprehensive collection in the world.

There are particularly good series of Ratites (including the Tinamidae), Cuculidae, and especially *Uria aalge*.

Special collections

In addition to the systematic series, some collections are kept separately:

Eggs of varieties of domestic poultry.
Six eggs of *Pinguinus impennis*.
Stuart Baker's collection of *Cuculus canorus*. It has not been practicable to incorporate in the main collection the eggs in all the boxes of this species.
Chance Collection, still in its own cabinets.

Geographic coverage

Most collecting occurred when the colonial powers of the northern hemisphere were in their heyday. This is reflected in museum collections of that period, and those of the NHM are particularly rich in African and Indian material. Local and national museums may have more complete local collections but few, if any, have the general coverage of the NHM. However, where we have indicated that the Museum's coverage is weakest, it should not always be assumed that better collections exist elsewhere. Degree of coverage is given below by regions.

Western Palaearctic. Very good.

Eastern Palaearctic. Not good. The best represented area is Japan from whence the collector Owston sent a considerable amount of material to Rothschild. There are also collections by Katsumata from Hainan and Tancré from central Asia (particularly the Altai and round Issyk Kul Lake). All of these were received with the Rothschild bequest. The Museum also holds the collections of La Touche, Rickett, Styan and Swinhoe; these are mainly from south China.

Middle East. Patchy and poor. Some good collections from southern Iraq and the northern end of the Persian Gulf, but otherwise comparatively little.

Africa north of the Sahara. Poor. There are collections made by expeditions to Morocco under Salvin, Tristram and others in the 1850s and by Rothschild and Hartert in the early years of the 20th century. Some collectors such as Aharoni collected in the Sahara (and also in the deserts of the Middle East) but these collections are small.

Afrotropical Africa. Good, but patchy. Parts of east Africa were well worked by collectors such as Benson and Pitman, but there is very little from west Africa. Angola and Gabon are represented solely by material from Ansorge, a botanist who collected anything he found, including quite a number of birds with their nests and eggs. He apparently knew little about birds and the identifications were made later; there is thus a small element of doubt with some. From South Africa there are the Layard collections (usually with no data) of the nineteenth century, and one or two small collections such as that of Bernard Jupp.

Burma and the Indian sub-continent. Excellent. Mostly the work of British Army officers and civil servants, these are probably the best in the world for this area; an incomparably rich collection.

Southeast Asia. Almost nothing except the E.G. Herbert and Sir Walter Williamson collections made near Bangkok, Thailand. Both contain good series of local species.

Indonesia. Almost nothing, this area formerly being under Dutch influence. There are collections by Whitehead and Sir Hugh Low, both from British Borneo, and the Steere Expedition specimens from the Philippines. This area is the most poorly represented in the whole Museum collection.

Melanesia and the Papuan regions. Not good. Rothschild's collectors moved through this area and collected extensively, but eggs were nowhere taken in quantity.

Australia and New Zealand. Not good. A number of eggs are of historic interest, particularly those from John Gould and Sir Walter Buller. A list of Australian eggs in the collection was drawn up in the 1960s prior to the Harold Hall Expeditions. This is no longer complete, due to more recent acquisitions.

Pacific Ocean. Poor overall, but there are long series of some species from particular islands, such as Norfolk, Lord Howe and the Galapagos. Many islands are not represented at all, and most are represented only poorly.

North America. Rather poor, mostly dating from the 19th century.

Central America. Very poor. Very little collecting seems to have been done here by the British, apart from Godman and Salvin during the last century.

South America. Very poor on the whole but, for a high proportion, the eggs of South American species are still unknown. There are good collections from Trinidad and the Falklands, and long series from places like Los Yngleses (a British-owned estate near Buenos Aires belonging to the Gibson family) but the general coverage is not good. Other important collections include those by Berkeley James from Chile, and Venturi from Patagonia.

In summary, the collection possesses probably the best assemblage of eggs of the Indo-Burmese area, and possibly the best general collection for Africa. It is weak in specimens from North and South America and Southeast Asia.

Some collections of particular interest

Stuart Baker collection. The largest collection of Indian eggs and, although a few specimens are suspect, some species are not known to be represented in any other collection.

T.R. Bell collection. A fairly large Indian collection, which arrived in its original boxes with each egg individually wrapped in cotton wool. Bell worked for the Forestry Commission in India in the late 19th and early 20th centuries. His field diaries are in the Entomology Library of the NHM at South Kensington.

Edgar Chance collection. Completely card-indexed, this collection arrived in its own cabinets. As it was well housed and beautifully laid out, it has never been incorporated with the main collection. Chance wrote several books on the Cuckoo.

Philip Crowley collection. At the turn of the century, this was the largest egg collection in private hands. A proportion of it was acquired by the Museum about 1901–2, the rest was dispersed and may now be lost. So, too, are his original catalogues. Some species are still, after nearly a century, represented only by eggs from this generous bequest.

J. Davidson collection. This large Indian collection was received about 1925 and, although much of it has been incorporated, a great deal remains to be done. Davidson had sorted and catalogued part of it after his return from India. A considerable amount seems never to have been unpacked, and reached the Museum in the original boxes in which it travelled back from India. The eggs had not been sorted into clutches, or even species. They are identifiable only by species numbers written on them, the numbers referring to one of 2 lists of Indian birds. Like Bell, Davidson apparently worked for the Forestry Commission in India.

J.H. Gurney collection. Incorporated in 1955, this was formerly at Norwich Castle Museum. It consists only of birds of prey and owls, but includes some species not otherwise represented in the collection.

A.O. Hume collection. The first large collection of Indian eggs, received in the 19th century. Hume was one of the most significant early contributors to Indian ornithology, and published his own journal *Stray Feathers*.

F.C.R. Jourdain collection. This huge collection must be one of the most important for the Palaearctic.

H. Munt collection. Henry Munt specialised in white eggs, and in eggs from birds in captivity (he seems to have been in close communication with many breeders). His collection contains many rarities. The collection was registered in 1941.

J.D. Salmon collection. Formed in the early nineteenth century, and donated to the Linnean Society in the 1860s, before subsequently coming to the Museum.

H. Seebohm collection. The earliest large collection of Palaearctic eggs.

Rödern collection. Count von Rödern's collection was acquired by Rothschild towards the end of last century. It was apparently accompanied by 2 catalogues: one printed, and a manuscript written by Max Kuschel, the well-known German oologist. These were last seen at Tring in the 1950s, when Glegg mentioned them in a note in the *Ibis* (1951: 305–6). They subsequently disappeared. The collection is poorly documented but contains some interesting specimens, including series showing wide ranges of colouring within selected species.

Eggs of particular interest

An egg of the extinct Syrian Ostrich *Struthio camelus syriacus*, which passed in turn from Charles Doughty to Col. T.E.Lawrence (Lawrence of Arabia) and Col. Richard Meinertzhagen.

The only known egg of the extinct Kangaroo Island Emu *Dromaius baudinianus*.

A clutch of eggs of the Emperor Penguin *Aptenodytes forsteri* collected by Cherry-Garrard (Cherry-Garrard 1922).

Two putative eggs of the extinct Labrador Duck *Camptorhynchus labradorius*. There are no eggs of this species whose authenticity is above question (*contra* Greenway 1967: 174; see also correspondence at Tring).

Type specimens of *Anthus venturi* and several putative species of *Megapodius*.

The only eggs of the extinct rails *Cabalus modestus* and *Pareudiastes pacificus*.

An English egg of the Great Bustard *Otis tarda* from the Montagu Collection; the Great Bustard last bred in England about 1840.

H.L. Popham's clutch of the Curlew Sandpiper *Calidris ferruginea*; this was the first clutch ever found of this species, and is still the Museum's only clutch.

Six eggs of the Great Auk *Pinguinus impennis*. The Museum also holds a number of plaster casts and models of Great Auk eggs, often carefully painted in the colour and pattern of particular specimens in other collections. There is also a remarkable fake, an egg of a swan which was painted to resemble that of a Great Auk. It was part of the J. D. Salmon collection (see above) and had been substituted for a real Great Auk egg in that collection, sometime between Salmon's death and the acquisition of his collection by the NHM.

Eggs (and nests) of the extinct Laysan Millerbird *Acrocephalus familiaris*.

Five eggs collected by Audubon. All seem to have been acquired by H.B. Tristram, whose collection passed to Crowley. The Museum received many of Tristram's eggs with the latter's bequest. The Museum also has Tristram's complete catalogues. It is probable that other Audubon eggs await discovery.

There are a number of eggs of other extinct species, together with specimens collected by well-known ornithologists such as Ayres, S.F. Baird, D. G. Elliot, Heermann and Krider. Many of these are without data and had been set aside as 'duplicates', although they have now been retrieved.

Unincorporated collections

Neglect of the egg collection during the early and middle 1900s led to a considerable backlog of incorporation. There are a number of valuable acquisitions, estimated at 30–40,000 eggs, which are still partially or entirely unincorporated. Since these are not in a state in which they could be used by visitors, this represents a great loss to the collection.

Col. E.A. Butler collection. A very good collection, mainly from India, Ceylon and northeast Africa. Registered but still only partly incorporated. Butler was an army officer who collected eggs as a hobby and published a number of papers. His collection was received by the Museum as part of the Rothschild bequest.

Chance collection. See 'Some collections of particular interest'.

Davidson collection. See 'Some collections of particular interest'.

Jourdain collection. Several cupboards contain the residue of this vast collection, which formed part of the Hewitt bequest (the rest of which is now at the Delaware Museum). The eggs were very mixed-up when they arrived at the Museum, and considerable numbers still cannot be matched with the relevant data.

Letchworth Museum collection. A mixed assemblage, but including some quite rare eggs of North American waders. Only partly incorporated.

Capt. Pitman collection. The late Captain C.R.S. Pitman, probably the most important east African collector, presented his eggs in small numbers over a period of time. Much has been incorporated, but some still awaits study.

H.L. Popham collection. An important Siberian collection; still only partly incorporated.

Rödern collection. See 'Some collections of particular interest'. A portion of this collection awaits incorporation.

South Kensington. A batch of eggs received about 1981 seems to be part of an old collection formerly in the public gallery. It includes a number of very old specimens registered prior to 1880 and not listed in Seebohm's ms catalogue (see below).

Tait collection. Put together by a well-known English ornithological family resident for some years in Portugal, and presented to the Museum some time after the death of the last surviving member living there. The eggs are very dirty and, until recently, were unsorted. The data slips (in Portuguese) have also become separated from the relevant clutches. This collection contained the only known eggs of the Guillemot *Uria aalge* from Portugal, and these have been incorporated.

William Borrer Tracy collection. British eggs of historic interest presented by Rear Admiral H.G.H. Tracy in 1979.

F.E.W. Venning collection. Venning worked mainly in Iraq, Pakistan and Burma, where he was one of the most important collectors. He was exceptionally meticulous. The collection was accompanied by detailed notebooks containing a wealth of data on each clutch, mainly relating to nest site and nest construction, incubation and so forth. It has only been partly incorporated, and most of Venning's valuable data seems never to have been published.

S. Venturi collection. A South American collection of great importance, written up by Hartert & Venturi (1909). Part of the Rothschild material. Most has been incorporated.

Waller collection. A large collection of general interest, received in the 1970s.

Whitehead collection. John Whitehead was a famous explorer and collector who visited and wrote about Mt Kinabalu, Borneo. He subsequently died while on an expedition to Hainan. His collection of European eggs was acquired by Rothschild and bequeathed to the NHM. Mostly incorporated, but a small part remains.

P.F. Wickham collection. A collection of Burmese eggs presented by Exeter Museum in the 1980s in exchange for some mounted skins.

The history and status of curation

The egg collection was last completely revised and catalogued in the 1890s, by Henry Seebohm. It was set out and labelled at this time by Miss Emily Mary Sharpe (Dr Bowdler Sharpe's daughter), since when many boxes remain unaltered. Seebohm prepared a manuscript catalogue (still held in the Egg Section) of all the specimens in the study collection. This did not include eggs in the public galleries and, in recent years, some of these have been retrieved and incorporated. The galleries were raided from time to time by members of the public, and many eggs are now lost.

Between 1901 and 1912 the 5 volumes of Oates's *Catalogue of the collection of birds' eggs in the British Museum (Natural History)* were published by the Museum (Oates 1901–12). They were based on Seebohm's manuscript, but included many additional specimens. The introduction to volume 1 contains further details of the history of the collection.

Curation of the collection over the subsequent 60 years seems to have been fitful, though a card-indexing system was started quite early on. Its coverage was no more than perfunctory and work seems to have ceased on it after a short time. Only a small number of the original cards have been found, mostly relating to birds of prey. They are beautifully written and demonstrate detailed and meticulous research. The writing appears to be that of the Rev. F.C.R. Jourdain.

Although Walter Rothschild's bird skins from Tring were sold to the American Museum of Natural History in 1932, he retained his sizeable egg collection. The latter passed to the Natural History Museum on his death in 1937, the largest acquisition ever received. During the 1940s, W.E. Glegg sorted and registered parts of it, a task continued by Mrs F.E. Warr in the 1950s. Rothschild's material was an assemblage of separate collections brought together by him, mainly by purchase.

Mrs Warr was also responsible for initiating the accessions index for the Museum's egg collection. For a time, Rachel Warren worked on parts of the Davidson material, but most of her cards have now been replaced. Some donors of small collections wrote their data directly on to Museum cards and these are preserved in the index. Envelopes, the same size as the cards and similarly printed, are used to hold original labels, letters or similar material relating to the relevant eggs.

In 1960 an attempt was started by C.J.O. Harrison and S. Parker to recatalogue and completely card-index the collection. From this date onwards all eggs received and incorporated—a considerable number—were card-indexed, and given a new style of label. Prior to the NHM's Harold Hall Expeditions (Hall 1974), all the Australian material was revised and card-indexed, mainly by Mr Parker, although more has since been added.

From 1970 onwards, MW has worked on incorporation and the systematic revision of the entire collection. Most of the cards from this period have been typed, whereas the bulk (though not all) of the previous ones are handwritten. The non-passerines and sub-oscine passerines have now been revised and card-indexed. Data extracted from the Seebohm and Oates catalogues have been added to the cards, and entries have been made (in red ink) for eggs no longer in the collection.

During the 1970s there was a series of systematic thefts by a visitor, Mervyn Shorthouse, who had been using the collection regularly. Between 1975 and 1979, an estimated 30,000 eggs were stolen before he was apprehended (and subsequently convicted). About 10,000 eggs were recovered, but the usefulness of many is limited, and the integrity of large parts of the egg collection has been jeopardised. As well as removing eggs, Shorthouse often substituted specimens from elsewhere in the collection to fill gaps and, in some instances, deleted and replaced registration numbers to conceal his activities. Many of the recovered eggs had data, set-marks and registration numbers removed from them, making it difficult to match the eggs with their data. The collection has since been carefully revised through to the Alaudidae. Until the revision is complete (which will take some considerable time), the remaining passerine eggs can only be used with great care.

The nest collection

The nest collection contains only about 2000 specimens, of which probably fewer than 200 are non-passerines. The coverage is poor in every way, although no detailed investigation has been carried out. It is less of a collection than an accumulation of miscellaneous material which happened to be deposited with the Museum over the years. Thus, there are quite long series of some Himalayan species (from H. Stevens), while many common British species are either unrepresented or represented by only one or two examples.

The nests have only been roughly sorted into families, and no catalogue has ever been made. The nests are stored in Tring cabinets, either loose in the plastic trays or in glass-topped boxes.

THE REGISTERS AND CATALOGUES OF THE BIRD COLLECTIONS

The registers and the catalogues of the Museum collections fulfil quite separate purposes. The registers contain details of specimens, entered as they are acquired (or curated), and usually arranged in blocks of specimens received together. The catalogues contain details of specimens arranged in a systematic, or similar, order.

The Old Catalogue

The earliest extant list of the collection is a thick catalogue volume with pages watermarked '1813', compiled by Dr W.E. Leach. Each page was numbered and used for a different species, with the specimens listed in columns down the right-hand side. Some specimens were indicated by letters of the alphabet. A synonymy with references was given for each species. This volume is referred to as the *Old Catalogue*, and appears to have been in use from 1813 (or shortly afterwards) until about the commencement of the *Vellum Catalogues*. A note, probably by J.E. Gray or J.G. Children, referring to this Catalogue is to be found tipped in at the beginning of *Vellum Catalogue* volume 5. It explains some of the entries and indicates species that were wanting in 1824.

The Vellum Catalogues

Most of the entries from the *Old Catalogue* also appear in the more comprehensive *Vellum Catalogues*, which were mainly compiled by G.R. Gray. The paper in these volumes is watermarked 1832, 1833 and 1834. The *Vellum Catalogues* were not apparently maintained beyond 1837. Forty of the 44 volumes in the series are divided into 15 sets covering the major groups of birds. Within each set, the right hand pages are numbered consecutively, one for each species of bird, for which a partial synonymy, without references, was also given. Individual specimens were identified by different letters of the alphabet. The registration number 12.177b is therefore *Vellum Catalogue*, volume 12, species (page) no. 177, specimen 2. The other 4 volumes (numbered 1–4) were used for British birds, and do not strictly belong with the remainder of the series. In the time of G.R. Gray, volumes 5–44 of the *Vellum Catalogues* were known as the *General Catalogue*, and the sets were identified with Roman numerals; reference to an entry took the form: xii 177b.

The General Registers

The main registers began in 1837 as a combined vertebrate series. These are referred to as the *General Registers*. Registration numbers originally comprised 4 groups of digits, the first 3 being the year, month and day of registration, and the last being the specimen number on that day, for example, 1842.5.17.16. Birds continued to be registered in the *General Registers* until 1853. A single Vellum register of birds was maintained by G.R. Gray for 1837–8. It mainly consists of the same bird entries as are found in the *General Registers* for that period, but also has some which are not found there.

The Aves Registers

In 1854 the separate *Aves (Bird) Registers* were started, although bird skeletons were usually included with the rest of the vertebrates for several decades to come. Numbers in the *Bird Registers* follow the same format as described for the *General Registers*, until the 1940s, when the use of 3 groups of digits was introduced: the year of registration, a number allocated to each collection, and the number of the individual specimen within that collection, e.g. 1945.64.202. This change took place in July 1943 for eggs, and January 1945 for other specimens. A few large collections were identified differently: e.g. 1949.WHI.1.1-17450 for the Whistler collection; 1955.6.N.20.1-4931 for the Gurney collection from Norwich Castle Museum and 1965.M.1-19575 for the Meinertzhagen collection.

Separate registers were used for part or all of several very large collections: Hume (3 volumes, 1885–95); Salvin & Godman (5 volumes, 1885–1913); Tweeddale (1887–92); Seebohm, Hargitt (1 volume, 1896–7); Simons (1902); Styan, McConnell (1 volume, 1907–22); Witherby, Ticehurst (1 volume, 1934, 1941); Whistler (1949); Gurney, birds of prey (the original Norwich Castle Museum catalogue into which a NHM registration number prefix was placed before each catalogue number [1889] 1955); Meinertzhagen (1965); and Hewitt (1969). Some confusion was incurred by the use of separate registers, and duplicate numbers are often found.

During the present century, most of the bird entries for the period 1837–53 were copied out of the old *General Registers*, into a separate volume of the *Bird Register* which is now used at Tring.

There are currently 29 volumes in the main Aves series, with a 30th in progress, and 17 volumes of special collections. Most run to 300–400 pages, with about 50 lines per page. Up to the end of 1941, each *Aves Register* contains either one or two indexes to the donor and sellers of the collections listed therein. There is also a comprehensive index covering the period 1906–1920. A separate series of small, loose-leaf binders, listing donors/sellers (and their specimens) in alphabetical order, covers accessions from 1906 to the present. For the period prior to that, Sharpe (1906) gives an index, but it is not complete.

Aves accessions for 1837–93 have been listed chronologically (and in part duplicated), one line to each collection, in a manuscript volume entitled '*Zoological Accession; Aves; 1837–1893*'. This provides an additional means of tracing specimens without the need to scan the full registers.

The Skeleton Vellum Catalogues

Separate *Skeleton Vellum Catalogues* (18 volumes), similar in layout to the *Vellum Catalogues*, were maintained from about 1844 (watermarked on the paper of the first 15 volumes; the last 3 are apparently later) through to the 1880s. Species numbers ran consecutively through the whole set, so volume numbers are not needed to locate entries, which take the form 944a. Most specimens also have *General Register* numbers. The catalogues appear to have been compiled initially between 1844 and 1846, probably for the bird part of Gray (1847). Some original entries do not bear *General Register* numbers, and some skeletal material remained unregistered until the 1950s, when all previously unregistered bones were registered. The old numbers are still found on many of the bones.

Card indexes

Separate card-indexes exist for the skeleton and spirit collections, and were apparently maintained until the 1930s. The former runs to 9 drawers of 5 × 3 inch cards. The spirit index comprises 6 drawers, with a seventh containing miscellaneous entries. Both indexes bear cross-references to

R.B. Sharpe's *Hand-list* (Sharpe 1899–1909), and were started sometime after publication of that work.

The Egg Register

The register for eggs was separated gradually from the main skin series by 1916. Prior to that date, only the large Seebohm collection (1901) and a few others, from 1912 onwards, appear in the *Egg Registers*. There are now 5 volumes, with a sixth currently in use, as well as 3 catalogue volumes of the Munt collection (1941), into which Museum registration numbers have been inserted. In about the mid 1890s, Henry Seebohm compiled a 10 volume manuscript catalogue of the eggs in the Museum collection, apart, it seems, from those in the public galleries. It was never published, but formed the basis for Oates (1901–12). An alphabetical accessions register (of donors and sellers) for the egg collection was started in the 1950s. Further information on the egg collection (and details of the card-index to the collection) will be found elsewhere in this paper.

The Skeleton Register

The register for skeletons was separated in 1952. At about the same time, the entries for old skeletons were extracted from the *Skeleton Vellum Catalogues* and the *General* and *Aves Registers* in a separate volume. A few numbers were overlooked, but not many.

The Nest, Spirit and Domestic Bird Registers

The register for nests was separated in 1959 and that for anatomical specimens in 1969. Numbers in all these separate series follow the format described for the *General* and *Bird Registers*.

Much of the nest collection is still unsorted and unregistered. Although new nests are given standard 3-part numbers, the old, previously unregistered nests are now allocated 2 groups of digits (collection and specimen), prefixed N (e.g. N257.3). Some nests previously given numbers in either the *General* or *Aves Registers* have been subsequently re-registered in this latter style.

Between 1900 and 1920, a separate register was maintained for domestic birds, but only a few pages were ever used.

ACCESS TO THE COLLECTIONS AND LIBRARY

Potential visitors to Tring should write to the Officer in Charge, stating the object of their proposed visit. Access is normally restricted to those undertaking original scientific research intended for publication. For such visits there is no charge. Work with commercial implications, including that of artists working on bird books, incurs bench charges or other fees. Visitors are encouraged to build bench fees into grant applications where possible. The collections are not normally accessible to casual visitors, although open days are held from time to time. Loans are made only to recognised institutions, on the same basis as visitor access.

INFORMATION RELATING TO THE COLLECTION

Several catalogues have been compiled, of which Gray (1844–67, 1847, 1863), Oates (1901–12), Sharpe & others (1874–98), Warren & Harrison (1966–73) and Knox & Walters (MS) are the most important. In addition, there have been numerous guides to the specimens in the public galleries (often giving data), and detailed catalogues of individual collections received by the Museum. Some of the latter were published as books, and others as papers in journals. References are given above to surveys of the spirit and skeleton collections.

Biographical and historical

Much historical information, together with biographical sketches of many of the collectors and donors, can be found in Sharpe (1906). Additional material relating to authors and collections appears in each of the 3 volumes of the catalogue of type-specimens (Warren & Harrison 1966–1973). Edwards (1870), Gunther (1975, 1980) and Stearn (1981) give general histories of the Museum and many of the staff, while Miriam Rothschild (1983) describes in detail the life and work of her uncle, Walter, and his famous museum at Tring where the Bird Section is now housed. Although not written with the museum user specifically in mind, Mearns & Mearns (1988) provide biographies of a great many relevant authors and collectors.

Acknowledgements

Drafts of the manuscript were read by Mr I.R. Bishop, Mr N.J. Collar, Mr G.S. Cowles, Dr C. Violani and Mrs F.E. Warr. We are grateful for their comments.

References:

Blandamer, J. S. & Burton, P. J. K. 1979. Anatomical specimens of birds in the collections of the British Museum (Natural History). *Bull. Brit. Mus. (Nat. Hist.), Zool. ser.* 34: 125–80.

Cherry-Garrard, A. 1922. *The Worst Journey in the World, Antarctic 1910–1913.* 2 vols. London.

Clancey, P. A. 1984. Tring as an ornithological centre. *Bokmakierie* 36: 32–35.

Clench, M. H. 1976. Possible pitfalls in museum specimen data. *North American Bird Bander* 1: 20–21.

Cocker, M. 1990. *Richard Meinertzhagen: soldier, scientist & spy.* (paperback) London.

Conover, M. R. & Hunt, G. L. 1989. Interpreting the sex ratios of gulls using museum specimens. *Colonial Waterbirds* 12: 132–133.

Edwards, E. 1870. *Lives of the Founders of the British Museum.* London.

Foster, M. S. & Cannell, P. F. 1990. Bird specimens and documentation: critical data for a critical resource. *Condor* 92: 277–283.

Gray, G. R. 1844–1867. *List of the Specimens of Birds in the Collections of the British Museum.* 5 parts in 8 vols. London. A 2nd edition of part 1 was issued in 1848. This work was never completed.

— 1847. *List of the Osteological Specimens in the Collections of the British Museum.* London.

— 1863. *Catalogue of British Birds in the Collections of the British Museum.* London.

Greenway, J. C. 1967. *Extinct and Vanishing Birds of the World.* 2nd edition. New York.

Gunther, A. E. 1975. *A Century of Zoology at the British Museum, through the Lives of two Keepers, 1815–1914.* London.

— 1980. *The Founders of Science at the British Museum, 1753–1900.* Halesworth, Suffolk.

Hall, B. P. 1974. *Birds of the Harold Hall Australian Expeditions 1962–70.* London.

Hartert, E. & Venturi, S. 1909. Notes sur les Oiseaux de la République Argentine. *Novit. Zool.* 16: 159–267, pls. 2–3.

Knox, A. G. & Walters, M. P. (MS). *Extinct and Endangered birds in the Collections of the Natural History Museum.*

Mearns, B. & Mearns, R. 1988. *Biographies for Birdwatchers.* London.

Murphy, R. C. No date. *Journal of the Tring trip, from the Letters and other Notes of Robert Cushman Murphy, 1932.* Bound copies of letters, notes and cuttings, in the library at the NHM, Tring.

Nicholson, E. M. & Ferguson-Lees, I. J. 1962. The Hastings Rarities. *British Birds* 55: 299–384.

Oates, E. W. (& Ogilvie-Grant, W. R.) 1901–1912. *Catalogue of the Collection of Birds' Eggs in the British Museum (Natural History).* 5 vols. London.

Parkes, K. C. 1989a. Sex ratios based on museum collections—a caution. *Colonial Waterbirds* 12: 130–131.

— 1989b. Response to Conover and Hunt. *Colonial Waterbirds* 12: 220–221.

Peters, J. L. & others. 1931–1987. *Check-list of Birds of the World.* 16 vols. Cambridge, Mass.

Rothschild, M. 1983. *Dear Lord Rothschild.* Philadelphia & London.

Sharpe, R. B. 1899–1909. *A Hand-list of the Genera and Species of Birds.* 5 vols. London.

— 1906. Birds. Pp. 79–515 in, *British Museum, The History of the Collections Contained in the Natural History Departments of the British Museum.* Vol. 2. London.

— & others. 1874–1898. *Catalogue of Birds in the British Museum.* 27 vols. London.

Stearn, W. T. 1981. *The Natural History Museum at South Kensington.* London.

Van Tyne, J. 1952. Principles and practices in collecting and taxonomic work. *Auk* 69: 27–33.

Warren, R. L. M. & Harrison, C. J. O. 1966–1973. *Type-specimens of Birds in the British Museum (Natural History).* 3 vols. London.

Wood, D. S. & Jenkinson, M. A. 1984. *World Inventory of Avian Anatomical Specimens: geographical analysis.* Norman, Oklahoma.

— & Schnell, G. D. 1986. *Revised World Inventory of Avian Skeletal Specimens, 1986.* Norman, Oklahoma.

—, Zusi, R. L. & Jenkinson, M. A. 1982a. *World Inventory of Avian Skeletal Specimens, 1982.* Norman, Oklahoma.

—, —, —, 1982b. *World Inventory of Avian Spirit Specimens, 1982.* Norman, Oklahoma.

Addresses: Dr A. G. Knox, Buckinghamshire County Museum, Tring Road, Halton, Bucks, HP22 5PJ; M. Walters, Natural History Museum, Tring, Herts, HP23 6AP.

© British Ornithologists' Club 1992

Guidelines for the description of new species in ornithology

by Mary LeCroy & François Vuilleumier

Received 5 June 1992

Introduction

This paper has been written because of our disappointment with many descriptions of new species of birds which we felt were not up to the high standards we should expect in modern avian systematic work. In an attempt to remedy this problem, we present in this paper a set of suggested guidelines, the use of which, we believe, would improve the current situation significantly. A preliminary version of this paper was presented in poster form at the XXth International Ornithological Congress in Christchurch, New Zealand (LeCroy & Vuilleumier 1990).

After presenting the background and the data on the rate of new species descriptions in ornithology, we discuss the kinds of problems that exist, with descriptive examples, followed by a series of concrete and, we hope constructive, suggestions for future workers.

Background

About 35 years ago the catalogue of birds of the world at the species level appeared to be so nearly complete that Mayr (1957: 35) wrote: "I doubt that more than 20 new species will be discovered in the next ten years". Later, however, in view of the steady flow of descriptions of new species in the ornithological literature, Mayr (1971: 315) concluded that "the number of undescribed new species of birds is by no means nearly exhausted, contrary to my earlier predictions".

Asking "Why have all these [avian] species been overlooked so long?" Mayr & Vuilleumier (1983: 229) wrote "One reason is that some of them are sibling species . . .. Another, and more important reason, is that some of these [new] species have exceedingly small ranges . . ., or are restricted to virtually inaccessible places visited only recently by ornithologists . . .". Continued exploration of remote, and hitherto nearly inaccessible places, has indeed resulted in the description of unexpectedly interesting species mostly from tropical areas (see also Diamond 1985).

During the past 52 years ornithologists at the American Museum of Natural History (AMNH) in New York have published 6 reviews of new species of birds (Zimmer & Mayr 1943, Mayr 1957, Mayr 1971, Mayr & Vuilleumier 1983, Vuilleumier & Mayr 1987, Vuilleumier *et al.* this volume). These reviews can be undertaken because the AMNH houses the most complete bird collection in the world (about 830,000 skins and approximately 99% of the known 9000+ species) and offers the needed comparative material. Also, the rich library resources at AMNH permit us to have access to the vast majority of ornithological journals, even the most obscure and localized ones. The work done to prepare these reviews has given us the opportunity to examine critically all new species descriptions published in the last 5 decades.

Rate of new species descriptions

In the 52 years from 1938 to 1990, 291 new binomina have been proposed in the literature, of which c. 55% are probably valid full species (including allospecies *sensu* Amadon 1966), 18% are subspecies, 13% are synonyms, 1% are nomenclaturally invalid, 1% are hybrids and about 12% are *species inquirendae*. Over this period valid new species have thus been published at the rate of c. 3 species per year. This rate represents an annual increase of only 0.033% in the world's avifauna, an incredibly low figure. Probably in no other class of vertebrates are there so few as yet undescribed new species.

Given such a small number of new species being described annually, it is all the more essential that ornithologists should publish descriptions that are uniform, precise and scientifically of the highest calibre, thus leading the way for equally high calibre descriptions of new species in other disciplines. Unfortunately, too many descriptions of new species in ornithology, even in the 1980s and the present day, remain substandard. Clearly this state of affairs needs urgently to be changed.

The problem

While writing a chapter on the species concept in ornithology, one of us (Vuilleumier 1976) reviewed 107 new species descriptions for the period 1955 to 1974, and was struck by the relatively large number of poor descriptions of putative new species of birds. Later on, while preparing the last 3 reviews of new avian species (Mayr & Vuilleumier 1983, Vuilleumier & Mayr 1987, Vuilleumier *et al.* this volume) there was continued dismay at the mediocre quality of the work of some fellow ornithologists.

Thus, Vuilleumier & Mayr (1987: 146) wrote: "The authors deplore the practice of some ornithologists to describe allegedly new species of birds without reference to a type specimen. Far too often, the description of new species of birds is published in very obscure journals, at times even in privately printed journals. New species of birds should be all described in widely read, easily accessible, and preferably refereed ornithological journals. This would certainly eliminate the necessity of spending much time tracking down names that eventually turn out to be nomina nuda or synonyms . . ." A few examples will illustrate what these authors meant and what we mean in the present paper.

1. On 2 occasions, swallows (Hirundinidae) from Africa have been described as new on the basis of a single specimen obtained from flocks of migrants (Williams 1966, Fry & Smith 1985). Thus nothing is known of the breeding locality of these birds and in a group as difficult and widespread as the swallows, one cannot be sure that the proper comparisons have been made.

2. In other cases, putative new species have been described, again with inadequate documentation, and in obscure publications that we have had

much difficulty in finding, even in the comprehensive natural history libraries of the AMNH and the Museum of Comparative Zoology (MCZ). Thus *Crax estudilloi* was described in the *Game Bird Breeders, Aviculturists, Zoologists and Conservationists' Gazette* (see Vuilleumier & Mayr 1987: 140), which is not a professional ornithological journal, and *Asthenes luizae* was published in Volume 1, number 1, of *Ararajuba* (see Vuilleumier *et al.*, this volume). *Ararajuba* is the journal of the Brazilian Society of Ornithology, and although there is no question of its scientific calibre, it is unfortunately not yet widely circulated outside Brazil, and an important new record could thus have been easily overlooked.

3. In yet other instances, reading the description has proved almost impossible because of the language in which it was originally described (e.g. Vietnamese: *Lophura hatinhensis*—see Vuilleumier *et al.*, this volume).

4. We have reviewed cases where the 'types' were live (cage birds) at the time of description or publication (e.g. *Hypochera lorenzi* and *H. incognita*—see Mayr & Vuilleumier 1983: 222). These birds belong to a notoriously difficult group where species limits are very difficult to draw, and the absence of designated type specimens means that the new species are impossible to evaluate. Frequently also, such captive birds fail to be preserved when they die (see *Crax estudilloi*—Vuilleumier *et al.*, this volume).

5. A few years ago, the late Augusto Ruschi published no fewer than 4 poorly crafted descriptions of alleged new hummingbird species from Brazil, leaving such a confusing trail of problems that the correct identity of these birds is only now beginning to be understood (Hinkelmann 1988).

6. Perhaps the most striking example of inadequate presentation of a new species is illustrated by the recent description of *Laniarius liberatus* (Laniidae) from Somalia based chiefly on an analysis of DNA from blood samples and feather quills. The only known individual was caught in Africa, transported to Europe, and later transported back to, and released, in Africa, but, incredibly, not where it had been originally captured (Smith *et al.* 1991). Furthermore, this case is interesting because it received extensive coverage, including notes in *Trends in Ecology and Evolution* (Hughes 1992a,b, Peterson & Lanyon 1992), a piece in *BBC Wildlife* (Scott 1991), 2 letters in *Oryx* (Ansell 1992, Bourne 1992) and even a long article in the *New York Times* by Carol Kaesuk Yoon in the Science Section of 28 April 1992.

This specimen was doubly wasted. Its survival in a strange area after a year in captivity is highly unlikely and its ability to find a mate and reproduce is even more unlikely. Thus it was returned to the wild to die. Nor is there now any voucher specimen for the sample of DNA or a type specimen to serve as a standard of reference for the application of the new name. Believing in the good faith of the authors is not sufficient; it is a basic tenet of the scientific method that the availability of documentation and specimens is essential to permit others to assess the quality and accuracy of a scientist's work. That only one individual was seen in no way implies that the 'new' species is on the verge of extinction, or even rare. We highly recommend a recent article on the importance of collections and collecting, which was in fact published before the appearance of the description of the shrike (Winkler *et al*. 1991).

We feel that the standards of species description in ornithology, instead of improving, may be declining. Even professionally trained ornithologists are publishing bad descriptions of putative new species, while too many untrained ornithologists publish 'new' species in very local journals.

We wish to emphasize here that there are, and have been, excellent descriptions of new species in the literature. As models for good descriptions of new species of birds (without implying a judgment on the validity of the new taxon) we can cite those of *Stachyris latistriata* (Gonzales & Kennedy 1990) from the Philippines, *Meliphaga hindwoodi* (Longmore & Boles 1983) from Australia, *Pyrrhura orcesi* (Ridgely & Robbins 1988) from Ecuador, and *Cercomacra manu* (Fitzpatrick & Willard 1990) from Peru. We congratulate the authors of these and other similarly good descriptions, and suggest that these descriptions ought to serve as models for other workers.

In many countries where amateur ornithologists are numerous (Europe, USA), committees of specialists examine critically each sight record of a bird species allegedly identified as rare or new for that country. On the basis of the merit of each case, some of these records are accepted but others are simply rejected. We do not advocate the establishment of an international committee of reputable avian systematists who would similarly review critically each new species description, but we feel that high standards must be adhered to. Instead we present below deliberately explicit guidelines in order to help raise standards in the future. However, the clear distinction between species descriptions and discussions of species concepts first needs emphasising.

One of us (Vuilleumier 1976: 50) remarked earlier that new species of birds had very often been described by authors according to a morphological or typological species concept. At the time, Mayr's (1963b) biological species concept (and see Mayr 1982) was probably accepted by these authors, as opposed to some today (e.g. Cracraft 1983, McKitrick & Zink 1988) who prefer a phylogenetic one. All these concepts, and their relevance to systematics, classification, and speciation analysis, have been admirably covered by Haffer (1986, 1990) and need not be discussed further.

In the earlier instalments on new avian species, although judgment was passed on the validity of the new species of birds we reviewed, judgment was *not* passed on the species concept represented by each of those new species. Nor is this so in the present article, our goal being only to express our concerns about the standards of description of new species, without reference to species concepts.

The International Code of Zoological Nomenclature

The starting point for professional practice is clearly the *International Code of Zoological Nomenclature* (ICZN). J. Chester Bradley in the Preface to the first edition of the ICZN (1961) wrote the following:

"Like all language, zoological nomenclature reflects the history of those who have produced it, and is the result of varying and conflicting practices . . .. Ordinary languages grow spontaneously in innumerable directions; but biological nomenclature has to be an exact tool that will convey a precise meaning for persons in all generations."

The rules, recommendations and code of ethics of the ICZN (3rd ed, 1985, or subsequent editions) should be followed in the description of all new species of birds. It is important to point out in particular that:

(a) The Code does *not* infringe upon taxonomic judgement, or determine the rank to be given a population, but that

(b) The Code *does* promote stability and universality in the scientific names of animals, including birds, and provides, in the words of the Code, "a Name-Bearing Type" which is the specimen that provides an "objective standard of reference whereby the application of the name of a taxon can be determined". In the original description of a new species-level taxon this may be either:

(i) a *holotype*: a single specimen (or *the* single specimen) designated to bear the proposed name, or

(ii) a *syntype*: each specimen in the series mentioned in the description, when no holotype is designated.

Guidelines on what to publish

We list below the minimal number of items that we feel are absolutely necessary for inclusion to create a good description of a new species of bird.

1. Holotype or syntypes should be designated. To facilitate future comparisons and permit measurements to be made, we feel strongly that it is imperative that the type(s) be specimen material and not illustration, bits of feathers, or blood or tissue samples. The latter can be useful in many ways, but are no substitute for a type specimen, only additional evidence (see below). Additional specimens in a type series are highly desirable because they illustrate population variability.

2. Minimal information should include the catalogue number and the name of the institution where the type is deposited, the sex and age of the type specimen(s), the collecting locality in as much detail as possible, including coordinates and altitude, the date of collection, name(s) of collector(s), measurements and a detailed word description of the type(s).

3. Desirable additional information that may be the necessary basis upon which to judge the validity of the new species includes voice recordings, blood samples, tissue samples, anatomical specimens, notes on behaviour, ecology, etc.

4. The etymology and gender of the name proposed must be given.

5. Explanation should be given as to why the new species is included in a given existing genus, or why it is placed in a new genus. Comparisons should be detailed, and substantiated with adequate material such as figures or tables, and maps.

6. Comparisons made should be the appropriate ones; similar and/or related sympatric and allopatric forms should be compared in detail with the new species, maps should be included to illustrate the geographical relationships with precision.

7. Discussion of the biogeography of the genus in which the new taxon is placed is highly desirable, thus identifying the eco-geographic context of the new species within or among previously known species. Whether the new species is geographically disjunct, or is an allospecies (*sensu* Amadon 1966) or is an isolated species, should be discussed.

8. Why the new taxon, if allopatric, is a new species and not a new subspecies and what species concept is being followed in this instance should be explained.

Publishing a proposed name

New species of birds should be described in refereed journals whose editors are thoroughly familiar with the proper format for the description of a new taxon and with the ICZN. This will ensure that the necessary information for correct description is included and also will bring the proposed new taxon readily to the attention of the scientific community. It would be the responsibility of the editor to verify that the new species description submitted for publication conforms to the format advocated here, and which we hope can be accepted universally.

Although it is perfectly understandable that authors of new species should wish to publish such descriptions in their native language, today the *lingua franca* of science is English. Nearly all ornithologists can read English, even if they do not speak it. Hence a publication in the English language, or at least a thorough summary in English, would ensure, and to the author's benefit, that the description of a newly proposed taxon can be made available to as wide an international audience as possible. We strongly condemn the practice of some ornithologists of publishing new descriptions in books or catalogues, where they may be easily overlooked.

Deposition of type(s)

Because types are so important in basic systematic work, several rules must be followed for their true designation. They include:

1. The type(s) should be deposited in a recognized museum with good facilities for proper permanent storage of specimens and with an interest taken in care and preservation of type specimens on the part of professionally trained curators. It is of little use to anyone to keep the type in a private collection.
2. The type(s) should be labelled in a way that makes the special status of a type specimen immediately apparent; the type(s) should preferably be kept separate from the general collection.
3. Bibliographic reference to the published description and the proposed name should be clearly written on the label.
4. Since types are such crucial and essential repositories of systematic and biological information, yet are probably not loaned safely because of the vagaries of modern mails, they should be housed in institutions that can be visited relatively easily by ornithologists.

Discussion

We agree with Peterson & Lanyon (1992) that the best kind of new species description is a detailed one which includes a variety of types of information, backed up by type specimens. Interestingly, included in the *New York Times* article mentioned above is a list of the minimal items of information needed for an adequate description, from sources provided by Richard C. Banks of the U.S. Fish and Wildlife Service, Washington, D.C. It is most gratifying to see that Banks' list conforms in all ways with our own views, as expressed in this paper.

Conservation cannot proceed without detailed knowledge of avian diversity, and this can only be acquired by judicious sampling of populations and careful systematic analysis of collections. Given the current rate of habitat destruction, we wish to note here that conservationists who are against such sampling are jeopardizing their own efforts by hampering the acquisition of vital knowledge before it is too late.

As Mayr pointed out 30 years ago, avian biologists, including amateurs, have been leaders in several fields of biology in the past; in systematics this leadership could be accomplished because of the "completeness of the knowledge of birds" and especially because "most bird species are not merely known but also abundantly sampled from throughout their range" (Mayr 1963a: 30). However, it is becoming increasingly apparent as habitats are being destroyed at an alarming rate, that very many bird species are still insufficiently sampled and incompletely known and that the availability of discerningly collected specimens is more critical now than ever before. If we are to retain this status of leadership in the specialised branch of systematics which consists of describing new species-taxa, ornithologists must practice self-discipline and must follow a minimum number of rules. We hope that ornithologists who intend to describe new species of birds in the future will find our guidelines in this paper useful. If we want to avoid ridicule, we must avoid the kind of work that we still see too often published, even by colleagues who should know better.

Acknowledgements

We are grateful to James Monk for his constructive criticisms of a draft of this paper and we thank Elizabeth De Jesus for typing the manuscript.

References:

Amadon, D. 1966. The superspecies concept. *Syst. Zool.* 15: 245–249.

Ansell, W. F. H. 1992. To collect or not to collect—a conservation issue? *Oryx* 26: 119.

Bourne, W. R. P. 1992. Of shrikes, shrews and storm-petrels. *Oryx* 26: 119–121.

Cracraft, J. 1983. Species concepts and speciation analysis. Pp. 159–187 *in* R. F. Johnston (ed.), *Current Ornithology*. Vol. 1. Plenum Press, New York.

Diamond, J. M. 1985. How many unknown species are yet to be discovered? *Nature* 315: 538–539.

Fitzpatrick, J. W. & Willard, D. E. 1990. *Cercomacra manu*, a new species of antbird from southwestern Amazonia. *Auk* 107: 239–245.

Fry, C. H. & Smith, D. A. 1985. A new swallow from the Red Sea. *Ibis* 127: 1–6.

Gonzales, P. C. & Kennedy, R. S. 1990. A new species of *Stachyris* babbler (Aves: Timaliidae) from the Island of Panay, Philippines. *Wilson Bull.* 102: 367–379.

Haffer, J. 1986. Superspecies and species limits in vertebrates. *Zeitschr. Zool. Syst. Evolutionsforsch.* 24: 169–190.

— 1990. Ornithologists and species concepts. *Proc Int. 100 DO-G Meeting, Current Topics Avian Biol.*, Bonn 1988: 57–60.

Hinkelmann, C. 1988. Comments on recently described new species of hermit hummingbirds. *Bull. Brit. Orn. Cl.* 108: 159–169.

Hughes, A. L. 1992a. Avian species described on the basis of DNA only. *Trends Ecol. Evol.* 7: 2–3.

— 1992b. Reply from Austin Hughes. *Trends Ecol. Evol.* 7: 168.

International Code of Zoological Nomenclature. 1961. 1st ed. International Trust for Zoological Nomenclature, London.

International Code of Zoological Nomenclature, 1985. 3rd ed. International Trust for Zoological Nomenclature, Univ. California Press, Berkeley.

LeCroy, M. & Vuilleumier, F. 1990. Guidelines for the description of new species in ornithology. [Abstract.] *Acta XX Congr. Internat. Ornithol.* (*Suppl.*): 378.

Longmore, N. W. & Boles, W. E. 1983. Description and systematics of the Eungella Honeyeater *Meliphaga hindwoodi*, a new species of honeyeater from central eastern Queensland, Australia. *Emu* 83: 59–65.

McKitrick, M. C. & Zink, R. M. 1988. Species concepts in ornithology. *Condor* 90: 1–14.

Mayr, E. 1957. New species of birds described from 1941 to 1955. *J. Orn.* 98: 22–35.

— 1963a. The role of ornitholgical research in biology. *Proc. XIIIth Internat. Ornithol. Congr.*: 27–38.

— 1963b. *Animal Species and Evolution.* Cambridge, Massachusetts, Harvard Univ. Press.

— 1971. New species of birds described from 1956 to 1965. *J. Orn.* 112: 302–316.

— 1982. Processes of speciation in animals. Pp. 1–19 *in* C. Barigozzi (ed.), *Mechanisms of Speciation.* Alan R. Liss, New York.

Mayr, E. & Vuilleumier, F. 1983. New species of birds described from 1966 to 1975. *J. Orn.* 124: 217–232.

Peterson, A. T. & Lanyon, S. M. 1992. New bird species, DNA studies and type specimens. *Trends Ecol. Evol.* 7: 167–168.

Ridgely, R. S & Robbins, M. B. 1988. *Pyrrhura orcesi*, a new parakeet from southwestern Ecuador, with systematic notes on the *P. melanura* complex. *Wilson Bull.* 100: 173–182.

Scott, K. 1991. World first: bird survives baptism. *BBC Wildlife* 9 (8): 534.

Smith, E. F. G., Arctander, P., Fjeldså, J. & Amir, O. G. 1991. A new species of shrike (Laniidae: *Laniarius*) from Somalia, verified by DNA sequence data from the only known individual. *Ibis* 133: 227–235.

Vuilleumier, F. 1976. La notion d'espèce en ornithologie. Pp. 29–65 *in* C. Bocquet, J. Génermont & M. Lamotte (eds.), *Les Problèmes de l'Espèce dans le Règne Animal.* Tome I. Soc. Zool. France, Mém. no. 38. Paris.

Vuilleumier, F. & Mayr, E. 1987. New species of birds described from 1976 to 1980. *J. Orn.* 128: 137–150.

Williams, J. G. 1966. A new species of swallow from Kenya. *Bull. Brit. Orn. Cl.* 86: 40.

Winkler, K. W., Fall, B. A., Klicka, J. T., Parmelee, D. F. & Tordoff, H. B. 1991. The importance of avian collections and the need for continued collecting. *Loon* 63: 238–246.

Zimmer, J. T. & Mayr, E. 1943. New species of birds described from 1938 to 1941. *Auk* 60: 249–262.

Address: François Vuilleumier & Mary LeCroy, American Museum of Natural History, Department of Ornithology, Central Park West at 79th Street, New York, NY 10024–5192, U.S.A.

© British Ornithologists' Club 1992

Behavioural traits as an aid to solving taxonomic problems

by Hans Löhrl & Ellen Thaler

Received 30 April 1992

Until the end of the last century taxonomists relied entirely on morphological data obtained from skin collections. An article by Whitman (1898) entitled "Animal behavior" was the first publication to appear on this subject and accordingly attracted much attention. Later, the behaviour of the Anatidae was studied by Heinroth (1910), and thereafter, especially from 1927 and 1930 onwards, Lorenz published numerous papers, including (1941) reporting a comparative study of the behavioural patterns of 20 different species of the Anatinae, which considered the behaviour of females, males and young birds separately.

The methods employed in Lorenz's studies on tame ducks living under natural conditions were of a pioneering nature. Thereafter, all behavioural studies were carried out on birds kept under natural conditions, or by observing wild birds from a hide. Subsequently the literature on ethology has been voluminous.

However, in order to derive a taxonomic interpretation from behaviour, it has first to be decided which aspects of behaviour from which functional system are suitable for this purpose. Obviously of little value are behavioural components that are strongly influenced by abiotic and biotic environmental factors (such as climate, temperature, day length, form of vegetation, food supplies etc). Furthermore, we know that certain ecotypes, such as those of aquatic birds and birds of the high mountains, or those living in rocky regions, invariably exhibit convergent specific adaptations to their particular environment. We are, therefore, limited to behavioural traits that are influenced to a minimal degree by the environment, e.g. nest building, brood care, nestling behaviour, and to some extent also social behaviour and certain calls. All aspects of behaviour connected with obtaining food, on the other hand, on account of their high susceptibility to adaptive radiation, should be treated with caution. Nevertheless, certain elements of such behaviour can be extremely informative, such as the use of the foot in manipulating food, or other special adaptations. The greater the number of functional systems for which behavioural differences can be demonstrated, the more informative are these results for our present purpose.

Behavioural comparisons in the Regulidae

The classification of the family Regulidae recommended by Sibley & Ahlquist (1985) was not entirely acceptable. Additional uncertainties arose from a re-evaluation of the genetic differentiation of the American twin species *Regulus satrapa* and *R. calendula* by Ingold *et al.* (1988). On the basis of their investigations the authors claimed that the 2 species are "not closely related", which, as they pointed out, had already been

TABLE 1
Breeding and other behaviour in 4 species of *Regulus* to demonstrate the many differences in *R. calendula*

Goldcrest *R. regulus*	Firecrest *R. ignicapillus*	Golden-crowned Kinglet *R. satrapa*	Ruby-crowned Kinglet *R. calendula*
Social behaviour			
in migratory and wintering flocks	same	same	same
contact sleep			no contact sleep
Breeding			
territorial; hanging nest	same	same	same
Nesting material			
very fine	same	same	also stalks and leaves
Courtship			
no courtship feeding	courtship feeding	courtship feeding	no courtship feeding
Nestling nutrition			
mainly collembola, tiny arthropods	soon larger prey	same as *ignicapillus*	same as *ignicapillus*
Nestling			
down on head	same	same	no down
Nestling period			
(days): 22	22–24	19–20	18–19
Nestling behaviour			
huddle together after leaving nest;	same	same	do not huddle after leaving nest;
return to nest for 1–2 days	same	same	do not return to nest
Territorial song			
typical for Regulidae	same	same	atypical in frequency and phrasing

claimed by Mayr & Short (1970). Assuming that the 2 species reached the American continent at different times, Ingold *et al*. concluded that the "DNA data suggest that the Ruby-crowned Kinglet [*R. calendula*] is the most recent arrival". If, however, the 2 species are judged on the basis of their behaviour, and if they are compared in a similar way with the European twin species *R. regulus* and *R. ignicapillus*, it is impossible to agree with Ingold *et al*.'s conclusion (see Thaler 1988) (Table 1). E. Mayr (pers. comm. 1988) also expressed his doubts: "surely this Ruby-crowned kinglet arrived in North America long before the Gold-crowned [*R. satrapa*], not the reverse . . .".

The most striking differences in behaviour between *calendula* and the other 3 species are seen, for example, in connection with display (Fig. 1), which, although always species-specific, only in *calendula* differs entirely from the Regulidae pattern (Thaler 1988), as also in its song (see also Mayr 1956). In addition only in *calendula* do some of the first-year males regularly show delayed maturation plumage (i.e. may moult into a second juvenile plumage) (Thaler in press), whereas the other Regulidae species avoid intraspecific aggression in their first year by 'behavioural mimicry' (i.e. concealing the orange in their crown and behaving like females) (Thaler 1979, 1990). The complete absence of nestling down in *calendula* probably further differentiates it from other Regulidae. Thaler (1988) showed that *ignicapillus* has more primitive behavioural patterns than *regulus* and is most probably the common ancestor of all Regulidae. It would seem therefore that *calendula* has evolved from *ignicapillus* and in isolation in America has since acquired the differentiating characteristics which separate it from *satrapa*, the later arrival which has differentiated little as yet.

Behavioural traits of *Leptopoecile sophiae*

Although Severtzov's Tit Warbler *Leptopoecile sophiae* is no unfamiliar species (see Ali & Ripley 1971/2, Dementiev & Gladkov 1954), our knowledge of its behaviour is incomplete and its systematics still await clarification. Nicolai & Wolters (1971) placed *Leptopoecile*, presumably on account of its minute size, among the Regulidae, in whose vicinity it was also placed by Hartert (1916) and Stresemann *et al.* (1937). Schäfer (1938) placed it close to the tits, particularly to the Aegithalidae. The genus was not considered by Sibley & Ahlquist (1985). One of us has kept 4 pairs of *Leptopoecile sophiae* in aviaries since 1990, and it seems that *Leptopoecile* had not previously, at least for any length of time, been kept in aviaries. A wealth of unknown behavioural details was to be expected and was observed. Their social behaviour appeared highly developed and ritualized, and the existence of social courtship behaviour and group 'helpers' can be assumed. *Leptopoecile*, like *Regulus*, feeds on arthropods and, because it inhabits thickets, they also appear to have certain similar foraging strategies, since these are influenced by the environment. Nevertheless, when carefully observed they prove to differ fundamentally in feeding habits. *Leptopoecile* uses its feet (Fig. 2), tending to a similarity with the Aegithalidae (cf. e.g. *Aegithalos concinnus*—Löhrl 1985), with which they also share social behaviour and nest-building characteristics (Table 2).

Behavioural comparisons between the Sittidae and Paridae

The nuthatches (Sittidae) and the tits (Paridae) provide good examples of the fact that purely morphological studies do not necessarily yield unequivocal results. Hartert (1910–1922), convinced that these 2 families

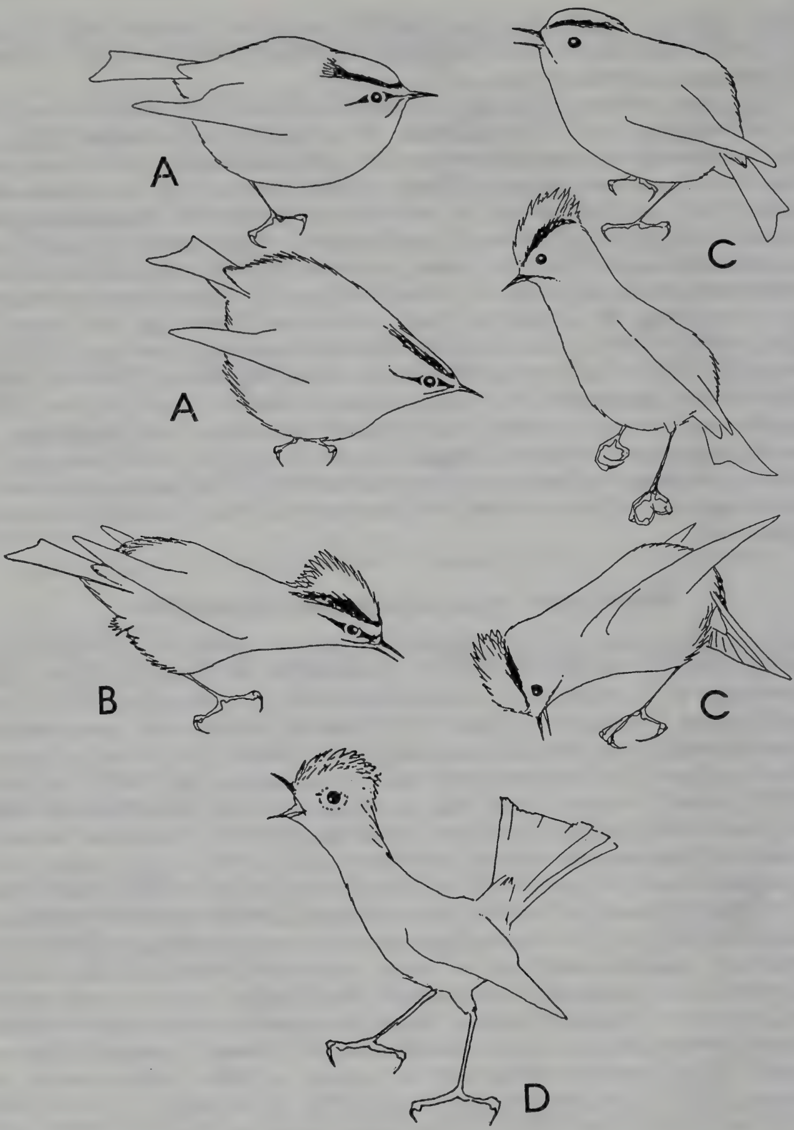


Figure 1. Threatening behaviour of (A) *Regulus ignicapillus*, (B) *R. ignicapillus* and *R. satrapa*, (C) *R. regulus* and (D) *R. calendula*. Adapted from Thaler-Kottek (1986).

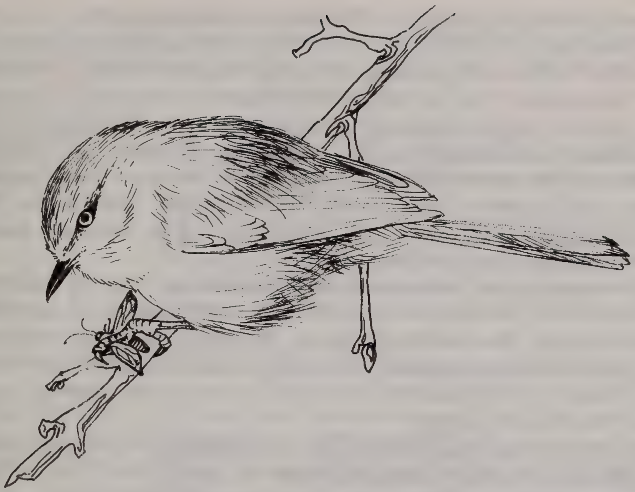


Figure 2. Severtzov's Tit Warbler *Leptopoecile sophiae* manipulating a moth by use of the foot.

TABLE 2

Breeding and other behaviour comparisons in *Leptopoecile sophiae*, Regulidae and Aegithalidae

Leptopoecile sophiae	Regulidae	Aegithalidae
Social behaviour		
year-round social or group territoriality ('helpers'?)	seasonally monogamous	year-round social or group territoriality ('helpers')
Nesting site, type of nest		
in bushes, oven-shaped nests	in trees, bowl-shaped, hanging nests, opening above	in bushes and trees, oven-shaped nests, supported or hanging
Courtship		
no courtship feeding	courtship feeding in *ignicapillus* and *satrapa*	no courtship feeding
Food		
arthropods	arthropods	arthropods
Foraging		
uncovers hidden food	eats visible food only	uncovers hidden food
Feeding strategies		
uses feet, even clamps prey; searches ground by scattering litter and turning over leaves	feet never used; prey 'killed' by banging	uses feet; does not search ground
Vocalizations		
clicking, purring	pure, high-pitched notes	clicking, purring

were closely related, placed the Paridae immediately after the Sittidae. A similar view was held by Vaurie (1959), who brought the Paridae even closer to the Sittidae by placing the latter as a subfamily, Sittinae, in the Paridae. However, this sequence was again completely altered on the basis of purely morphological considerations by Wolters (1975–1982), in his principal publication. For him, the Sittidae and Paridae were unrelated and far removed from one another. Between them he placed, for example, the extensive families of Nectariniidae, Estrildidae, Ploceidae and Emberizidae, and even the Sylviidae—as a separate family—are considered before the Paridae.

The distance placed between the nuthatches and tits by Wolters clearly shows that even the most conscientious examination of morphological characteristics of dead animals is, on its own, an inadequate means of arriving at reliable systematic conclusions. Following DNA hybridization studies, Wolters (1983) did in fact modify his views, placing the Sittidae nearer to the Paridae again.

Table 3 gives a comparison of the breeding and feeding habits of tits and nuthatches, based on detailed observations (Löhrl 1958, 1964, 1974, 1991). The behavioural traits cited are partially dependent on breeding site and environment. Inhabitants of tropical and subtropical regions gather no food reserves (e.g. Velvet-fronted Nuthatches *Sitta frontalis* and probably the African tit species). In Europe the Great Tit *Parus major* and the Blue Tit *P. caeruleus* do not lay up stores, but compensate for winter population losses resulting from food shortage by producing large numbers of offspring.

Behavioural traits of *Tichodroma muraria*

The Wallcreeper *Tichodroma muraria* was formerly grouped with the treecreepers (Certhiidae), e.g. by Hellmayr 1903, Hartert 1910–1922, due to false interpretation of their similar bills. Later it was considered as a subfamily of the Sittidae (Vaurie 1959, Peters 1967, Sibley & Ahlquist 1985) or even to be a distinct family (Voous 1977, Wolters 1975–1982).

Behavioural traits can only be taken as evidence of possible affinities if they are not ecological adaptations. In this particular specialist of high mountain regions, however, most of its characteristic movements are adaptations to its habitat. This is also true of its manner of seeking food and its flight. The exceptionally large wings permit the bird to exploit updraft to transport it from the depths of gorges into the upper regions. In searching for a behavioural trait of the Wallcreeper that is with certainty not an adaptation to its habitat, the possibility of a close affinity to the nuthatches was suggested by their similar attitudes in inter- and intra-specific conflicts; both the Wallcreeper and nuthatches adopt the same threatening posture, letting their wings hang and holding their tails erect (Fig. 3). Such a posture is seen in neither tits nor treecreepers. In addition, during the breeding season a gliding form of flight is observed in all nuthatches and also in the Wallcreeper (Löhrl 1988).

On the other hand, other forms of nuthatch behaviour, such as the way they handle food or, with the exception of tropical species, the laying-up of food stores, distinguish nuthatches from the Wallcreeper so clearly that

TABLE 3
Comparison of behavioural traits of tits (Paridae) and nuthatches (Sittidae) (but see text)

	Similarities	
Breeding behaviour	*Nests* in holes in trees, the holes enlarged to the required size where necessary. In larger holes the nesting space is partially filled with moss or wood. Cracks in the walls are stopped up with nesting material. *Nesting material*: moss, wool, feathers, pieces of bark. *Eggs* covered up with nesting material before incubation begins. *Incubation* of completed clutch can be postponed by as much as a week in periods of bad weather. *Courtship feeding* of female by male during nest-building period. *Young* fed by both parents. *Long nestling period*: 18–23 days.	
Feeding behaviour	Summer: insects and spiders. Winter: spiders, insects and plant diet. Sometimes lay up stores. Hidden food reserves sometimes covered up. Seeds sometimes deposited on a branch before storing.	
Other behavioural traits	Wing flicking when excited. Distraction behaviour: droops, waves and spreads wings and tail.	
	Differences	
	Tits	Nuthatches
Breeding behaviour	Incubation 12–15 days. Defends brood by complex defence behaviour: hissing, flapping wings against sides of hole, bill-snapping.	Incubation 15–18 days. Reduces size of entrance to nest with mud, for security.
Feeding behaviour	Breaks up hard food items while gripping with toes.	Breaks up hard food by pushing it into cracks and hammering with bill.

a separate family for *Tichodroma*, which should follow the Sittidae, seems to be ethologically justified.

Behavioural traits of *Siphia strophiata*

The affinities of the small flycatchers, which are common species in Asia, present special problems. In his generic revision of the Muscicapini Vaurie (1953) divided them mainly between the genera *Ficedula, Niltava* and *Muscicapa*. Originally, most of them had been placed in the genus *Muscicapa*—a classification still widely adhered to (e.g. by Ali & Ripley 1972, Etchécopar & Hüe 1983). Earlier taxonomic studies of these species, apart from morphological peculiarities or a comparison of habitats, were restricted to the observation that flycatchers "catch insects in the air", which holds equally for all 77 species treated by Vaurie, while even today,

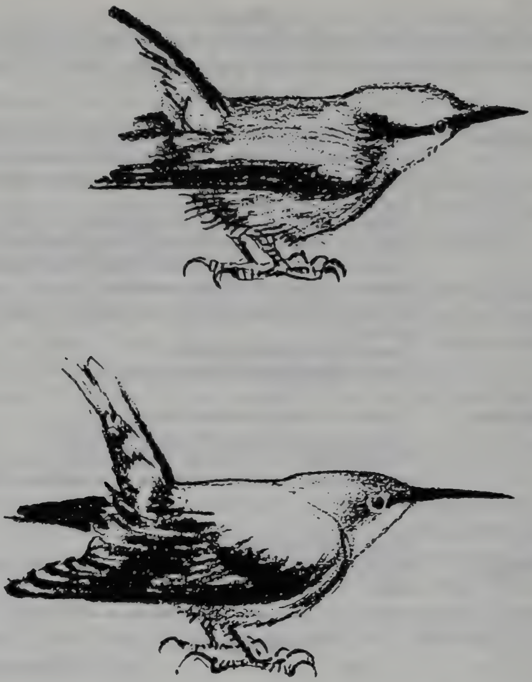


Figure 3. Threatening behaviour of the European Nuthatch *Sitta europaea* (top) and Wallcreeper *Tichodroma muraria* (bottom).

few details of their breeding biology have been described. The accurate observation of differences in behaviour under species-adequate aviary conditions is both possible and rewarding. The Orange-gorgeted Flycatcher *Siphia strophiata* is a good example, as decribed below.

The systematic position of *S. strophiata* is still controversial: in Hartert (1910–1922) it was termed *Muscicapa strophiata* and Vaurie (1953) considered it "appears to be not too distantly related to the Ficedula group". His decision was made mainly on the basis of morphological characteristics, although he was open to a consideration of such behavioural traits as were available.

Observations on *S. strophiata* kept in cages and aviaries over a considerable number of years revealed a most unusual method of obtaining food, otherwise seen mainly in limicoles (Löhrl 1992). By means of vibrating foot movements the birds shake the twigs on which they are perching and thus mobilise at the surface hidden prey. This is an innate foraging movement, since it was observed not only in several imported mature birds, but also in a young, aviary-hatched, hand-reared individual that had subsequently been isolated and thus had received no 'instruction' from an adult. *S. strophiata* is the only species of flycatcher so far known to use this method, and presumably thus secures itself an advantage over other species. It was not only this unusual method of prey-catching that raised the suspicion that this was not a 'normal' *Muscicapa* or *Ficedula* species. The bird's song resembles rather that of the Bluethroat *Luscinia svecica*, or the Robin *Erithacus rubecula*, and its frequent tail twitching is also seen in the Robin. The impression that its behaviour hardly resembles that of a flycatcher remained unaltered over the 8 years during which one of us observed a number of these birds; no visiting ornithologist thought these birds were a species of flycatcher, and most of them guessed that they were a species of thrush.

The removal of this species from the other flycatcher genera and its renaming (Wolters 1975-1982) as *Siphia strophiata* is fully justified from the ethological point of view.

Discussion

Behavioural patterns can be a useful supplementary help in clarifying some taxonomic questions. It seems that even very advanced techniques such as DNA hybridization are not entirely immune to subjective interpretation or free from errors. Only by considering the bird as a whole are we in a position to ask meaningful questions. Although it may be an exciting idea to take apart such a complex organism and then to attempt to reassemble it as if it were a puzzle, this involves the danger of losing sight of the overall picture, and perhaps also our feeling for the harmony of the whole.

References:
Ali, S. & Ripley, S. D. 1971, 1972. *Handbook of the Birds of India and Pakistan, together with those of Nepal, Sikkim, Bhutan and Ceylon*. Vols. 6–8. Bombay.
Dementjev, G. P. & Gladkov, N. A. 1954. *Birds of the Soviet Union*. Vol. 6. Moscow.
Etchécopar, R. D. & Hüe, F. 1983. *Les Oiseaux de Chine—Passereaux*. Paris.
Hartert, E. 1910–1922. *Die Vögel der Paläarktischen Fauna*. Berlin.
Heinroth, O. 1910. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. *Verh. Intern. Ornith. Congr. Berlin*: 615.
Hellmayr, C. E. 1903. *Das Tierreich 18, Aves: Paridae, Sittidae und Certhiidae*. Berlin.
Ingold, J. L., Weight, L. A. & Guttmann, S. I. 1988. Genetic differentiation between North American Kinglets and comparisons with three allied Passerines. *Auk* 105: 386–390.
Löhrl, H. 1958. Das Verhalten des Kleibers (*Sitta europaea caesia* Wolf). *Z. Tierpsychol*. 15: 191–252.
— 1964. Verhaltensmerkmale der Gattungen *Parus* (Meisen), *Aegithalos* (Schwanzmeisen), *Sitta* (Kleiber), *Tichodroma* (Mauerläufer) und *Certhia* (Baumläufer). *J. Ornith*. 105: 153–181.
— 1974. *Die Tannenmeise*. Neue Brehm-Bücherei 472. Wittenberg-Lutherstadt.
— 1985. Die Rostkappenschwanzmeise (*Aegithalos concinnus*). *Gef. Welt* 109: 334–335.
— 1988. Etho-ökologische Untersuchungen an verschiedenen Kleiberarten (Sittidae). *Bon. Zool. Monogr*. 26: 1–208.
— 1991. Die Haubenmeise, *Parus cristatus*. Neue Brehm-Bücherei 609. Wittenberg-Lutherstadt.
— 1992. *Siphia strophiata*, der Zimtfleckschnäpper. *Tropische Vögel* 13: 3–8.
Lorenz, K. 1927. Beobachtungen an Dohlen. *J. Ornith*. 75: 511–519.
— 1931. Beiträge zur Ethologie sozialer Corviden. *J. Ornith*. 79: 67–127.
— 1932. Betrachtungen über das Erkennen der arteigenen Triebhandlungen der Vögel. *J. Ornith*. 80: 50–98.
— 1941. Vergleichende Bewegungsstudien an Anatinen. *J. Ornith. Erg. Bd*. III: 194–293.
Mayr, E. 1956. *Gesang und Systematik*. Beitr. Vogelkunde 5.
Mayr, E. & Short, L. L. 1970. *Species Taxa of North American Birds*. Cambridge, Mass. Publ. Nuttall Orn. Club 9.
Nicolai, J. & Wolters, H. E. 1971. *Vögel in Käfig und Voliere*. Vol. 2. Aachen.
Peters, J. L. 1967. *Check-list of Birds of the World*. Cambridge, Mass.

Schäfer, E. 1938. Ornithologische Ergebnisse zweier Forschungsreisen nach Tibet. *J. Ornith.* 86, Sonderheft.

Sibley, C. G. & Ahlquist, J. E. 1985. The Phylogeny and Classification of the Passerine Birds, based on Comparisons of the Genetic Material DNA. *Acta XVIII. Congr. Int. Orn. Moscow:* 83–121.

Stresemann, E., Meise, W. & Schönwetter, M. 1937. Aves Beickianae. Beiträge zur Ornithologie von Nordwest-Kansu nach den Forschungen von Walter Beick (+) in den Jahren 1926–1933. *J. Ornith.* 85.

Thaler, E. 1979. Das Aktionssystem von Winter- und Sommergoldhähnchen (*Regulus regulus, R. ignicapillus*) und deren ethologische Differenzierungen. *Bonn. Zool. Monogr.* 12: 1–151.

— 1988. Etho-ökologische Differenzierungen bei amerikanischen Goldhähnchen: *Regulus satrapa, Regulus calendula. Proc. Int. 100. DO-G Meeting, Current Topics Avian Biol.* Bonn.

— 1990. *Die Goldhähnchen.* Neue Brehm-Bücherei 597. Wittenberg-Lutherstadt.

Thaler-Kottek, E. 1986. The genus *Regulus* as an example of different survival strategies: adaptation to habitat and etho-ecological differentiation. *Acta XIX Congr. Int. Orn. Ottawa:* 2007–2020.

Vaurie, C. 1953. A generic revision of flycatchers of the tribe Muscicapini. *Bull. Am. Mus. Nat. Hist.* 100. New York.

— 1959. *The Birds of the Palearctic Fauna. Passeriformes.* Witherby: London.

Voous, K. H. 1977. *List of Recent Holarctic Bird Species.* British Ornithologists' Union, London.

Whitman, C. O. 1898. *Animal Behavior.* Biol. Lect. Mar. Biol. Lab. Wood's Hole 285.

Wolters, H. E. 1975–1982. *Die Vogelarten der Erde.* Berlin.

— 1983. *Die Vögel Europas im System der Vögel.* Baden-Baden.

Addresses: Dr Hans Löhrl, Bei den Eichen 5, D-W-7271 Egenhausen, Germany; Prof. Dr Ellen Thaler, Alpenzoo, Weiherburggasse 37, A 6020 Innsbruck, Austria.

© British Ornithologists' Club 1992

Barriers, contact zones and subspeciation in central equatorial Africa

by Michel Louette

Received 31 January 1992

African forest and savanna avifaunas are recognised as being different, at least since Chapin's (1923) authoritative paper. Ecological vicariants do exist, but the number of biological species, composed of separate taxa, making contact in the forest/savanna border areas is restricted, *contra* Endler (1982). In fact, only few examples have been documented: e.g. *Scopus umbretta* (Bates 1931, Louette 1981), *Apaloderma narina* (Clancey 1959) and *Campethera caillautii* (Prigogine 1987). Similarly, the contact montane/lowland forest coincides very rarely with subspecies contacts: *Dendropicos elliotti* is one of the few examples (Louette 1981). There are, however, some superspecies contacts in both cases (see Prigogine 1980), but far less than Endler seems to admit.

In the present paper, we are concerned with examples to show differing contacts within the central lowland forest itself, the region from southern Cameroon to eastern Zaïre (Fig. 1).

The ranges of forest birds and savanna birds penetrating forest in equatorial Africa were mapped in the *Atlases* by Hall & Moreau (1970) and Snow (1978). Some additions were made by Snow & Louette (1981) and Louette (1984, 1987, 1988, 1988a, 1989). These and other papers cited should be used to illustrate the ranges of several birds given as examples below; but an incomplete positioning of contact zones between subspecies in Africa was given by Meise (1975) and by Mayr & O'Hara (1986) and a general examination of the ranges in order to identify possible barriers is long overdue.

Barriers and contact zones

Some African birds are able to leave their habitat temporarily (many Holarctic migratory forest birds, of course, do so): e.g. the long-distance migratory savanna nightjars *Caprimulgus rufigena* and *Macrodipteryx vexillarius* cross the forest twice after the breeding season, breeding only in the south. But there are almost no migratory African lowland forest birds.

I listed elsewhere (Louette 1990) the 216 stenotopic forest species. The selection was arbitrary. Here I want to mention that for some at least, the wrong decision seems to have been taken: *Telacanthura melanopygia, Neafrapus cassini, Eremomela turneri, Muscicapa tessmanni* and *Nectarinia cyanolaema* are indeed also forest birds, according to my own definition. Moreau (1966), Forbes-Watson (1970) and Amadon (1973) came to comparable figures. In any case, the degree of stenotopy varies within the group. I counted 156 stenotopic species covering virtually the whole forest block, leaving only a minority with restricted range therein. These contemporary ranges (and those of some other, eurytopic species) are

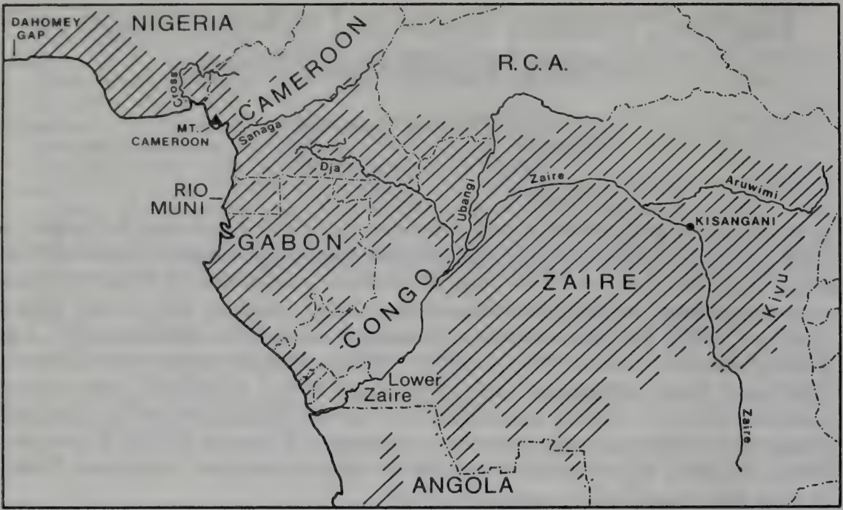


Figure 1. Central equatorial Africa. The Lower Guinea rainforest block is indicated with oblique barring.

considered to be positions taken up after radiation from a refuge and probably still dynamic (Mayr & O'Hara 1986). Suspected present day, as well as past, barriers (except for the presence of a vicariant species) include: degrees of altitude; inimical vegetation surrounding a refuge; savanna; hostile habitat in general: rivers and marsh. Examination of the ranges of such siblings as *Estrilda nonnula* and *E. atricapilla* allows one to presume that several such factors can act simultaneously (vicariants, philopatry, altitude, non-forest habitat, . . .).

Competition with other species cannot explain the peculiar distributions of the stenotopic forest birds (nor the eurytopic savanna birds mentioned below), because usually no congeneric species are involved. The polyspecific forest genera *Bleda* and *Malimbus* (the latter including 2 superspecies) were examined on this account, but no proof of competitive exclusion was found (Louette 1991a). However, the possibility of recent range restrictions or differences in ecological potential between the different parts of the forest cannot be excluded (Louette 1990). The restricted ranges are situated in particular areas outlined below, for which Louette (1990) produced a list of species (*pace* that given by Mayr & O'Hara 1986, which contains numerous errors, including the ranges for *Glaucidium sjoestedti, Spermophaga poliogenys, Merops breweri, Nectarinia adelberti* and others). These restricted ranges cover:

1) the whole of Upper Guinea or Lower Guinea, supporting the strong impact on distribution of the Dahomey gap in western Africa, a present day savanna wedge in the forest (Bates 1931, Moreau 1966);

2) particular parts of Lower Guinea in Cameroon/Gabon, in the Zaïre basin proper (only a few), and in a small eastern area;

3) the coastal forest for 3 species: *Tauraco macrorhynchus*, *Gymnobucco calvus* and *Nectarinia fuliginosa*.

There being no obvious ecological reason for this pattern and assuming those species under 2) and 3) did in fact have time and opportunity to spread out in the adjoining apparently suitable habitat, but did not do so, there must be a historical reason. The study of philopatry, with its genetic causes, is still in its infancy (Greenwood 1987). Land areas with high diversity and endemism correspond to refuges and centres of evolution during dry climatic phases according to several authors quoted by Prance (1982) and Crowe & Crowe (1982). Crowe & Crowe lacked information on the non-existence of an earlier suspected range gap for several bird species (such as *Apaloderma aequatoriale*) in central Zaïre (Louette 1984). Mayr & O'Hara (1986) and Prigogine (1988) again discussed the refuges for birds specifically in this region and Prigogine accepted a Zaïre Basin refuge which was not admitted by previous authors. Colyn *et al.* (1991), basing themselves on Primate ranges in the same region, similarly do not find a (geographic) diversity gradient, accepting also a quaternary (central) fluvial refuge, south of the present middle Zaïre. We lack, however, information on possible barriers in the period since the last dry phase.

Range limitation for forest birds by rivers

In South America, Capparella (1991) finds a whole series of bird species limited in range by large rivers (hundreds of cases?), or with separate subspecies or proven genetic differentiates on each bank. In central Africa, a similar phenomenon caused by several rivers was shown by Colyn (1987, 1988) for Primates. So it is reasonable to enquire whether this factor applies in African birds.

Very few subspecies ranges are given as delimited by rivers by White (1960, 1961, 1962, 1963, 1965), but that this could be the case for, for example, *Glaucidium tephronotum, Tockus hartlaubi* and *Alethe diademata* could be inferred. The maps in the *Atlases* for, for example, *Gymnobucco peli/sladeni, Trichastoma albipectus/cleaveri, Apalis rufogularis* races and *Anthreptes fraseri* races, also do give this impression for the Zaïre river, but the limitation is probably due to coincidence, in the same way as the range of *Ceratogymna elata* or the contact zone of *Malimbus cassini/scutatus* is limited by the Sanaga river (Louette 1981). In the *Tauraco persa* superspecies, where the Ubangi/Zaïre was a suspected barrier (Snow 1978), *persa* crosses it in fact towards the east in 2 places (Snow & Louette 1981).

There seems to be a genuine case in the genus *Centropus: C. neumanni* lives north and *C. anselli* south of the Zaïre river in Zaïre, but *C. anselli* also on the right bank towards Cameroon. In addition, *C. neumanni* does not reach the southern Kivu—it is definitely a philopatric species. (The other contact in the superspecies, *C. anselli/leucogaster*, in Cameroon and without introgression, is not along a river—Louette 1981). In investigating whether a coucal population would be limited by a very broad river, at least several hundred metres wide in the stretch of river considered and with a quite stable regime (Devroey 1951) and containing forested islands, I found traces of introgression in the 'contact area', west of Kisangani, showing that the Zaïre river barrier is actually not absolute (Louette 1986).

Barriers by rivers seem to occur in African birds otherwise only in a few galliformes.

1)*Francolinus squamatus* and *F. ahantensis* are separated by the lower Niger (Elgood 1982).

2) *Guttera plumifera* is apparently squeezed by the Sanaga (Dejaifve 1991 mentions an unconfirmed sighting on the right bank) and the Zaïre rivers.

3) *Agelastes niger* lives from the Nigerian/Cameroon border in the west (Dejaifve 1991; limited by the Cross river?) to the right bank of the Zaïre (without penetrating towards southern Kivu).

4)*Afropavo congensis* has, in the opinion of all previous workers, a most puzzling range, present as it is on both banks of the Zaïre, but living in eastern Zaïre only. Verheyen (1962), suggested it is limited by the very humid soils in the western part of the Zaïrean (marsh) forest on the left bank, and by high altitude in the east. This may well be so; it is hard to believe that it would be excluded by the much smaller and even partly sympatric *Agelastes niger*, as suggested as plausible by Snow (1978). But why is it absent from the middle part of the right bank where the forest is 'dry', as in the bird's actual range (IUCN 1990)? Possibly these 2 species became trapped in pockets of forest on the 2 different banks of the Zaïre or Aruwimi rivers during a dry period, before spreading out and living now mostly, but not exclusively, on different banks.

The absence of both *Centropus neumanni* and *C. anselli*, and also *Agelastes niger* from the well forested southernmost Kivu suggests that this region was barriered from their refuge, configuration of the rivers perhaps prohibiting colonisation in this area by these 'philopatric' species avoiding large river crossings. To the contrary, *Afropavo congensis* was possibly on the right bank of the Zaïre, but later crossed it upriver from say Kisangani, penetrating to and beyond the left bank; it has crossed the Aruwimi as well (see map in Verheyen 1962).

It is noteworthy that other forest galliformes, in the genera *Guttera* and *Francolinus*, are not delimited by the entire Zaïre river. *F. lathami* shows a peculiar pattern of distribution, with the population in south-central Zaïre morphologically so similar to the one towards Cameroon/Gabon that it is considered consubspecific and different from the population more to the north in Zaïre, on the right bank of the Zaïre river (Louette 1984). This southern population must have arrived from the west (or *vice versa*), crossing the Zaïre river in its lower reaches, rather than arriving from the more plausible northern population; but the latter possibility may indeed have been excluded by the middle Zaïre river (or Ubangi river) being a barrier at the appropriate period. There are other examples of extension of races of strong flying lowland forest birds from western origin towards southern Zaïre or northern Angola or both, suggesting possibly simply another forest localisation formerly.

In contrast to Amazonia, it is clear that equatorial Africa does not have a river system separating bird populations to a great extent. A study of the genetic differentiation of all these species on both banks would be welcome.

Particular savanna species delimited by forest

One wonders what would be the barrier in the species where the range includes a particular part of the forest, though the largest part of the range is in savanna; an example of this distribution of eurytopic species is *Buteo auguralis* (Louette 1991). It migrates to rather high latitudes in the northern hemisphere in Africa. However, it is present (only as a migrant?) in the whole forested region of Upper Guinea and from western Cameroon towards northwestern Angola; it is absent towards the east in central and southern Zaïre in forest as well as in the periforest/savanna, although there is no vicariant. Other species with a rather similar distribution are not rare: *Agapornis pullaria, Colius striatus, Centropus monachus, Smithornis capensis, Chloropeta natalensis, Zosterops senegalensis* and *Poeoptera lugubris*. The fact that these eurytopic savanna birds occur in 'the Cameroon/Gabon forest refuge' and not in 'the Zaïre Basin refuge', augments diversity there and explains in part Crowe & Crowe's (1982) findings. However, in my opinion these species do not really belong to the forest avifauna. Further, their absence in accessible savanna points to a historical reason (and philopatry) for the peculiar distribution. But there may be an ecological one—maybe they do not penetrate into marshforest or into the deepest part of the forest block.

Haffer (1988) estimates c. 100 land bird species in Amazonia are limited to riverine surroundings in forest. Such a group exists also in forested central Africa, but its composition in species is much smaller: *Pseudochelidon eurystomina* (migratory), *Riparia congica, Nectarinia congensis* and *Quelea anomala*. These live only alongside the Zaïre and its major tributaries, apparently enclosed by 'hostile habitat (forest)' and unable to escape to possibly more favourable habitat elsewhere; Prigogine (1988) incorporates them in his group originating in the Zaïre Basin refuge, together with real forest birds with restricted range. There is a possible second type in the forest: *Bradypterus grandis* lives in riverine marshes along the Dja river (it occurs also in Gabon). Possibly an almost unknown species such as *Ploceus batesi* will reveal itself as also being confined to riverine forest habitat. Other typical riverine birds such as *Ploceus melanocephalus duboisi, P. pelzelni* and *Merops malimbicus* are not completely enclosed by the forest block, although they are restricted in range to central Africa. In addition there are other riverine species in central Africa, but surrounded by savanna (outside the scope of this paper), suggesting that the forest is a barrier by chance for the riverine group. Similarly, *Anthreptes gabonicus* and *Ploceus subpersonatus* are limited to mangroves, the last one to a very restricted part of them.

That forest can be a solid barrier is proven indirectly by the stenotopic savanna bird penetration from the northern woodland and savanna through a (former) corridor along the Ubangi river towards Lower Zaïre, such as *Dendropicos goertae* (Louette & Prigogine 1982). Other similar cases are *Numida meleagris, Caprimulgus climacurus, Crinifer piscator, Phoeniculus aterrimus* and *Batis minor* (Louette 1987). No differentiation, or only minor, has occurred suggesting recent immigration.

The surroundings of the lower Ubangi were even contemporarily not covered with forest, large 'ésobé' grasslands existing in this general area. These species definitely must have followed a western (central) route, because east of the forest belt the savanna connection is blocked by a vicariant. There are no examples of a penetration northwards (but possibly they would spread out rapidly and cannot be detected by examination of range maps). The last arid period seems to have culminated at 18,000 years BP (van Zinderen Bakker 1986), with semi-arid conditions in the 'central Congo' region. The aridity was of a magnitude much larger than needed to explain these penetrations, permitting a whole savanna fauna exchange. Probably *Francolinus coqui* (towards the north) and *F. albogularis* (towards the south) achieved the penetration during such a period. The present positioning of the savanna species in Lower Zaïre must have taken place much later (the equatorial forest reappeared from 9000 years BP—Maley 1989), with a corridor of grassland as a sufficient gateway. Also, the separation of the forest bird populations referred to above as being possibly due to the Zaïre river may simply have been produced by this vegetation corridor along the river, not by the river itself.

Subspeciation

Subspeciation within the Lower Guinea forest block proper is given in White's check-lists. He does not differentiate races based on colour or on measurements, nor abrupt and clinal ones. Since White's papers were written, no complete review of subspeciation in Africa has been made. Therefore we still use White's races provisorily to render geographical variation, although, no doubt, in many cases too few statistically valuable criteria were used to create them (see Barrowclough 1982).

Contacts between subspecies of forest birds, as for borders of species' ranges, are numerous in the general region of Mount Cameroon, clearly a suture line of an old non-forest gap (Louette 1981; but see Maley 1989, who postulates montane forest descending to lower levels here during part of the Quaternary). Some of the contacts are somewhat to the west, others to the east of Mount Cameroon (cf. Meise 1975), quite possibly a result of different colonisation speed rather than an indication of separate gaps (cf. Mayr & O'Hara 1986); also, the supposed influence of the Sanaga river may in fact be a consequence of this Mount Cameroon gap. Examples rather far to the east from the Mount Cameroon suture line include: *Lybius hirsutus, Pitta angolensis* and *Stiphrornis erythrothorax*. With the contact still more to the east is *Terpsiphone rufocinerea*, studied by Chapin (1953); equally *Alcedo leucogaster, Bycanistes fistulator, Psdalidoprocne nitens* and *Alethe poliocephala* qualify. Some western races are present in northwestern Angola, but for *Spermophaga haematina* the eastern race is there and I suggested a "push" from the western population in the southern Zaïre sector towards the east (Louette 1988). Subspecies bordering the Zaïre river were mentioned above. A former gap (savanna, ésobé grassland, lake, river?) in west-central Zaïre may explain these positions.

Clines in colour or dimensions or both are present in many forest birds, with the gradient changing from west to east somewhere in Zaïre (Louette

1991a gave several examples: e.g. *Andropadus latirostris*, *Bleda syndactyla* and *B. eximia*). (Others are morphologically homogenous throughout this part of the range, though differing elsewhere; for example *Andropadus virens*.)

The morphological differences in bird species in Lower Guinea (just as are those for Upper Guinea, listed by Bates 1931) do not contradict the refuge hypotheses. The contacts between (incipient) subspecies in Lower Guinea may be the result of both an east and a west colonisation from the Cameroon-Gabon and Albertine Rift refuges (which other species due to philopatry are still occupying solely—Crowe & Crowe 1982, Prigogine 1988). Possibly, however, some of the differentiation is due to adaptation to local conditions: the study of this phenomenon is far from finished (Boag & Van Noordwijk 1987).

References:

Amadon, D. 1973. Birds of the Congo and Amazon forests: a comparison. *In* B. J. Meggers, E. S. Ayensu, & W. D. Duckworth (eds). *Tropical Forest Ecosystems in Africa and South America: a comparative review*. Smithsonian Institution Press, Washington.

Barrowclough, G. F. 1982. Geographic variation, predictiveness and subspecies. *Auk* 99: 601–603.

Bates, G. L. 1931. On geographical variation within the limits of West Africa: Some generalisations. *Ibis* Ser. 13 (1): 255–302.

Boag, P. T. & Van Noordwijk, A. J. 1987. Quantitative genetics. *In* F. Cooke & P. A. Buckley (eds). *Avian Genetics*. Academic Press, London.

Capparella, A. P. 1991. Neotropical avian diversity and riverine barriers. *Acta XX Congressus Internationalis Ornithologici*: 307–316.

Chapin, J. P. 1923. Ecological aspects of bird distribution in tropical Africa. *Am. Nat.* 57: 106–125.

— 1953. The Birds of the Belgian Congo. *Bull. Am. Mus. Nat. Hist.* 75A: 1–821.

Clancey, P. A. 1959. Miscellaneous taxonomic notes on African birds. XII. *Durban Mus. Nov.* V(12): 151–179.

Colyn, M. M. 1987. Les Primates des forêts ombrophiles de la cuvette du Zaïre: interprétations zoogéographiques des modèles de distribution. *Revue Zool. Afr.* 101: 183–196.

— 1988. Distribution of guenons in the Zaïre-Lualaba-Lomami river system. *In* A. Gautier-Hion, F. Bourlière & J. P. Gautier (eds). *A Primate Radiation: Evolutionary Biology of the African Guenons*. Cambridge University Press.

Colyn, M., Gautier-Hion, A. & Verheyen, W. 1991. A re-appraisal of palaeoenvironmental history in Central Africa: evidence for a major fluvial refuge in the Zaïre basin. *J. Biogeogr.* 18: 403–407.

Crowe, T. M. & Crowe, A. A. 1982. Patterns of distribution, diversity and endemism in Afrotropical birds. *J. Zool.* (London) 198: 417–442.

Dejaifve, P. A. 1991. *Esquisse de l'avifaune du Parc National de Korup, sud-ouest Cameroun.* Mimeo report for Wildlife Conservation International, New York. 70 pp.

Devroey, E. J. 1951. *Atlas général du Congo. Notice de la Carte des eaux superficielles du Congo Belge et du Ruanda-Urundi*. Institut Royal Colonial Belge, Brussels.

Elgood, J. H. 1982. *The Birds of Nigeria*. British Ornithologists' Union, London.

Endler, J. A. 1982. Pleistocene forest refuges: fact or fancy? *In* G. T. Prance (ed). *Biological Diversification in the Tropics*. Columbia University Press.

Forbes-Watson, A. D. 1970. The avifauna of the African lowland forest and its eastern and western extremities (Kakamega, Kenya and Mt. Nimba, Liberia). *Abstract XV Congr. Int. Orn.*

Greenwood, P. J. 1987. Inbreeding, philopatry and optimal outbreeding in birds. *In* F. Cooke & P. A. Buckley (eds). *Avian Genetics*. Academic Press, London.

Haffer, J. 1988. Vögel Amazoniens: Ökologie, Brutbiologie und Artenreichtum. *J. Orn.* 129: 1–53.

Hall, B. P. & Moreau, R. E. 1970. *An Atlas of Speciation in African Passerine Birds*. British Museum (Natural History).

IUCN. 1990. *La Conservation des Ecosystèmes Forestiers du Zaïre*. (Basé sur le travail de Charles Doumenge). IUCN, Gland.

Louette, M. 1981. The Birds of Cameroon. An annotated check-list. *Verhandelingen Koninklijke Academie voor Wetenschappen, Letteren en Schone Kunsten van België. Klasse der Wetenschappen*, 43 (Nr. 163): 1–295.

— 1984. Apparent range gaps in African forest birds. *Proc. V Pan-Afr. Orn. Congr.*: 275–286.

— 1986. Geographical contacts between the taxa of *Centropus* in Zaïre, with the description of a new race. *Bull. Brit. Orn. Cl.* 106: 126–133.

— 1987, 1988, 1988a, 1989. Additions and corrections to the avifauna of Zaïre (1). *Bull. Brit. Orn. Cl.* 107: 137–143; (2). 108: 43–50; (3): 108: 112–120; (4): 109: 217–225.

— 1990. Distribution patterns in African lowland forest birds. *In*: G. Peters & R. Hutterer (eds). *Proceedings of the International Symposium on Vertebrate Biogeography and Systematics in the Tropics*. Museum A. Koenig, Bonn, Germany.

— 1991. The red-tailed buzzards of Zaïre. *Bull. Brit. Orn. Cl.* 111: 51–55.

— 1991a. Geographical morphometric variation in birds of the lowland equatorial forest of Africa. *Acta XX Congressus Internationalis Ornithologici*: 475–482.

Louette, M. & Prigogine, A. 1982. An appreciation of the distribution of *Dendropicos goertae* and the description of a new race (*Aves: Picidae*). *Rev. Zool. Afr.* 96: 461–492.

Maley, J. 1989. Late Quaternary climatic changes in the African rain forest: forest refugia and the major role of sea surface temperature variations. *In*: M. Leinen & M. Sarnthein (eds). *Paleoclimatology and Paleometeorology: Modern and past patterns of global atmospheric transport*. NATO ASI series. Kluwer.

Mayr, E. & O'Hara, R. J. 1986. The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. *Evolution* 40: 55–67.

Meise, W. 1975. Natürliche Bastardpopulationen und Speziationsprobleme bei Vögeln. *Abh. Verh. Naturwiss. Ver. Hamburg* 18/19: 187–254.

Moreau, R. E. 1966. *The Bird Faunas of Africa and its Islands*. Academic Press.

Prance, G. T. (ed). 1982. *Biological Diversification in the Tropics*. Columbia University Press.

Prigogine, A. 1980. Etude de quelques contacts secondaires au Zaïre oriental. *Gerfaut* 70: 305–384.

— 1987. Hybridization between the megasubspecies *caillautii* and *permista* of the Green-backed Woodpecker *Campethera caillautii*. *Gerfaut* 77: 187–204.

— 1988. Speciation patterns of birds in the Central African forest refugia and their relationship with other refugia. *Acta XIX Congr. Int. Orn.*: 2537–2546.

Snow, D. W. (ed). 1978. *An Atlas of Speciation in African Non-passerine Birds*. British Museum (Natural History)

Snow, D. W. & Louette, M. 1981. Atlas of speciation in African non-passerine birds. *Addenda* and *Corrigenda* 2. *Bull. Brit. Orn. Cl.* 101: 336–339.

van Zinderen Bakker, E. M. 1986. African climates and palaeoenvironments since Messinian times. *S. Afr. J. Sc.* 82: 70–71.

Verheyen, W. N. 1962. Quelques données concernant le dimorphisme sexuel, la distribution géographique d'*Afropavo congensis* Chapin ainsi qu'un essai de bibliographie générale. *Bull. Soc. Roy. Zool. Anvers* 26: 7–15.

White, C. M. N. 1960, 1962. A Check list of the Ethiopian Muscicapidae (Sylviinae). Parts I, II, III. *Occ. Pap. Natn. Mus. S. Rhod.* 24B: 399–430; 26B: 653–738.

— 1961. *A Revised Check List of African broadbills, pittas, larks, swallows, wagtails and pipits*. 1962. *A Revised Check List of African shrikes, orioles, drongos, starlings, crows, waxwings, cuckoo-shrikes, bulbuls, accentors, thrushes and babblers. 1963. A Revised Check List of African flycatchers, tits, treecreepers, sunbirds, white-eyes, honeyeaters, buntings, finches, weavers and waxbills*. 1965. *A Revised Check List of African non-passerine birds*. Government Printer, Lusaka.

Address: Dr. Michel Louette, Koninklijk Museum voor Midden-Afrika, B-3080 Tervuren, Belgium.

© British Ornithologists' Club 1992

Past and future taxonomic research in West Africa

by Gérard J. Morel & Claude Chappuis

Received 27 April 1992

In the opinion of Brown *et al.* (1982) only some 20 new species of birds have been discovered these last 20 years in the whole African continent, i.e. one species annually on average. Since discovery of new species is most likely in montane forests, where endemism is enhanced, and in regions where exploration is difficult, West Africa would appear at a special disadvantage in this respect. We shall review the forms (species or subspecies) new to science discovered in West Africa over the last 30 years, with emphasis on the new techniques—particularly bioacoustics—that give taxonomy a new impetus. For the Non-passerines, we have adopted the sequence of *The Birds of Africa*; for the Passerines, we have followed Bannerman (1953); for the new forms we use the names proposed by the authors; for *Stizorhina*, we have adopted the names given by Howard & Moore (1980).

The discovery of new forms can be attributed to 2 main techniques.

New forms from the study of skins

The study of skins, either obtained during recent exploration or of older origin, the classic technique, aided by morphological analysis, is still widely used.

PURPLE HERON *Ardea purpurea bournei* (Naurois 1966)

Compared with the nominate, *bournei* is very pale; the paleness of the first specimen that reached the British Museum was merely ascribed to bleaching (Bannerman & Bannerman 1968). Restricted to São Tiago island in the Cape Verde archipelago, its total population may be under 200 pairs. It builds its nest in trees and forages on dry, even stony ground. Not recognized by Brown *et al.* (1982).

GREY HERON *Ardea cinerea monicae* (Jouanin & Roux 1963)

Also a very pale form, with a population of 1000–2000 pairs, restricted to the Banc d'Arguin islands, Mauritania. Owing to its unique nesting behaviour (a scrape on the ground), to its entire life being spent in marine waters and its distinct plumage, it could be considered a full species (Mahé 1985). Considered a doubtful form by Brown *et al.* (1982).

SPOONBILL *Platalea leucorodia balsaci* (Naurois & Roux 1974)

Distinguished by its black bill without a yellow tip and by a near absence of yellow buff on the chest. Also restricted to Banc d'Arguin, with a population of several thousand pairs (Mahé 1985). The bulky nest is piled upon low clumps of Chenopodiaceae.

COE'S HONEYGUIDE *Melignomon eisentrauti* (Colston 1981–especially footnote p. 290; Louette 1981)

This new species is only the second within the *Melignomon* genus. Originally discovered by Serle (1959: 65) as early as 1956, then redescribed by Eisentraut in 1963, it was thought by both that their specimens were mere immatures of *M. zenkeri*. First described by Serle (1959) from Mount Nimba, Liberia, this honeyguide is certainly widespread in Upper Guinea forests. (Details of nomenclature and description by the 2 separate authors (Colston 1981, Louette 1981) are also given in Colston & Curry-Lindahl 1986.) (See Vuilleumier *et al.* this volume.)

[No English name given by author] *Phyllastrephus leucolepis* (Gatter 1985)

The type of this new species is represented by one specimen of undetermined sex, collected in Liberia, 6°12′N,8°11′W, in a "transitional zone between evergreen and semideciduous tropical rainforest". Several individuals were observed, usually in bird parties including bulbuls, sunbirds and malimbes. The olive brown wing shows 2 pale bars, which are diagnostic, as this bulbul forages through the twigs with half opened wings. It seems that the wing pattern is used as an optical signal. (See Vuilleumier *et al.* this volume.)

GREY-HEADED BRISTLE-BILL *Bleda canicapilla moreli* (Erard 1991)

Based on specimens collected in Lower Casamance, Senegal, differs by its paleness and its bill shape from the nominate form which is only found in forest, from Guinea to Nigeria.

AFRICAN REED WARBLER *Acrocephalus baeticatus guiersi* (Colston & Morel 1984)

A. baeticatus remained unrecorded west of Chad until as late as 1960, when it was found in Senegal (Morel & Roux 1962). Subsequently it was described as a new subspecies (Colston & Morel 1984). Its range remains unknown; since *guiersi* lives in reedbeds, a naturally discontinuous habitat, it could be isolated. Widespread also in Mali (Lamarche 1980–81) and localized in Niger (Giraudoux *et al.* 1988).

RUFOUS CANE-WARBLER *Acrocephalus rufescens senegalensis* (Colston & Morel 1985)

Based on skins, obtained in Senegal, where it seems to live mainly if not exclusively in reedbeds; in Cameroun it is also found in sugar-cane. In Senegal, the pairs were widely spaced. As a whole, *A. rufescens*, a secretive but vocal species, is poorly known in West Africa.

PECTORAL PATCH CISTICOLA *Cisticola brunnescens mbangensis* (Chappuis & Erard 1973)

Restricted to the montane region of Adamawa, Cameroun, where it inhabits meadows with very short grass on stony ground. It is of smaller size, lighter coloration, with upperparts less intensely streaked, than the nominate race, but the voice seems similar.

ANNA'S FOREST FLYCATACHER *Melaenornis annamarulae* (Forbes-Watson 1970)

A species of the forest canopy, discovered on Mount Nimba, Liberia, and also found in southwestern Ivory Coast.

IBADAN MALIMBE *Malimbus ibadanensis* (Elgood 1958)

Hitherto regarded as endemic in southern Nigeria, there is one record recognized now from Owerri, east of the lower Niger (Marchant *in* Bannerman 1949) but first identified as *M. cassini*. Similarly Bannerman mentions *cassini* from Ibadan, recorded by Marshall. With the recognition of *ibadanensis* as a distinct species (Elgood 1958), both Marchant and Marshall agreed their sightings were almost certainly of *ibadanensis*, and Field (1979) accepted *ibadanensis* as occurring at Owerri. Now it seems likely that recent records of *cassini* from Tafo, Ghana (♂♂ only) (Grimes 1987) are likely to have been sightings of *ibadanensis* (Elgood in press). Formerly not uncommon, but local, at forest edges, in secondary forest and even gardens; but in view of a 10 year gap without any records (Elgood 1988), the species has come to be regarded as "endangered" (Collar & Stuart 1985).

New forms from acoustical signals

This group comprises new subspecies or species discovered by means of acoustical analysis, i.e. with the assumption that voice—or significant elements of a bird's vocalizations—are specifically distinct. This technique is valuable: (1) when 2 forms are morphologicaly very similar (e.g. *Streptopelia roseogrisea/S. decaocto*); (2) when of 2 closely related forms, one breeds in the Palaearctic and the other in the Afrotropics (e.g. *Cuculus canorus/C. gularis*); (3) when a polymorphic species is widely distributed over the continent (e.g. *Eupodotis ruficrista*). The acoustical analysis is usually confirmed by a morphological study.

CRESTED BUSTARD *Eupodotis ruficrista savilei* (Chappuis *et al*. 1979)

The race *savilei*, only found in West Africa, is vocally so distinct from the 2 other races *gindiana* and *ruficrista* by reason of the frequency used and by the rhythm and structure of the phrasing that an observer familiar with the latter 2 races may wonder what bird he is listening to (Fig. 1). *E. r. savilei* shows differences also in colour pattern and in nuptial display. Chappuis *et al*. (1979) recommended restoring *savilei* to its previous specific status.

AFRICAN COLLARED DOVE *Streptopelia roseogrisea* (Chappuis 1974–1985)

Long considered a mere subspecies of the Eurasian Collard Dove *S. decaocto* (Heim de Balsac & Mayaud 1962, Mackworth-Praed & Grant 1970) because of similar plumage and size; but comparison of their songs and flight calls (Fig. 2) compels recognition of 2 distinct species (Chappuis 1974–1985), confirmed by Urban *et al*. (1986).

EUROPEAN CUCKOO *Cuculus canorus* and **AFRICAN CUCKOO** *Cuculus gularis*

Because of their nearly identical adult plumage and closely comparable songs, these 2 forms have been considered as conspecific by several authors (e.g. White 1965, Voous 1960). This opinion was, however, revised as a result of morphological differences found in the young (Payne 1977). Confirmation is found in acoustical differences, even though these are slight and in a species with strictly inherited song: in *canorus* the 2 (sometimes 3) notes are always on a descending scale, but in *gularis* always ascending or monotonous.

COMMON SCOPS OWL *Otus scops* and **AFRICAN SCOPS OWL** *Otus scops senegalensis*

Considered conspecific by Snow (1978) and also by Fry *et al.* (1988), the 2 are indeed morphologically close, but their voices are very distinctive (Chappuis 1974–85). In the last historical contact zone between these 2 forms before the last glaciation (i.e. in the north/south Sahara), there is an absence of frequency overlap in the song of these 2 forms, with a gap of 250 hz and also an absence of clinal variation of frequency, which is 1300 hz in southern Morocco (recent personal measurements) compared with 1000 hz in West Africa. These differences, more distinct and rigid *within* the last contact zone than away from it (Van der Weyden 1973), suggest an ancient separation, prior to the geographical isolation, by means of vocal separation of these 2 forms, which thus deserve specific status.

AFRICAN BARRED OWLET *Glaucidium capense etchecopari* (Erard & Roux 1983)

Smaller than the nominate race and more restricted to forest, *etchecopari* ranges from the forests of Mount Nimba, Liberia (its place of discovery) through the southern forest belt of Ivory Coast and is common in the Ndouci-Lamto area. Insufficient acoustical data originally led to the conclusion that the east and west African populations were specifically distinct; but further studies have shown that both forms have similar vocal signals and are therefore only subspecies (Chappuis 1974–85).

RUSTY BROAD-BILLED ANT-THRUSH *Stizorhina fraseri* and **FINSCH'S BROAD-BILLED ANT-THRUSH** *Stizorhina finschi*

These 2 rather similar forms present acoustical differences in both their songs and in their cries: lower pitch (frequency ratio of 1.8) and longer duration (ratio of 1.55) for *finschi* (Fig. 3). These differences, taken separately, exceed what is normally expected in 2 populations of one species occupying the Guinean and Congolese forest blocks; while taken together, they support the diagnosis of 2 populations whose acoustical isolation has been achieved and which should be treated as a superspecies.

PLAINTIVE CISTICOLA *Cisticola dorsti* (Chappuis & Erard 1991)

Formerly assigned to *C. ruficeps* as the subspecies *C. r. mongalla.* Compared with *C. ruficeps*, the newly named *C. dorsti* exhibits a number of subtle colour differences, a longer tail and smaller white tail spots. Acoustically *ruficeps* and *dorsti* have nothing in common (see sonagrams *in* Chappuis & Erard 1991). *C. dorsti* inhabits the grass steppe with low bushes of northwestern Nigeria, northern Cameroun and southern Chad. It lives in sympatry with *C. ruficeps guinea.*

RIVER PRINIA *Prinia fluviatilis* (Chappuis *et al.* in press)

First found on the Upper Niger in 1969, now also in Chad and more recently in northwestern Senegal, its range remains to be elucidated. The song of the River Prinia was (and certainly remains) confused with that of the Tawny-flanked Prinia *P. subflava*. In *fluviatilis* there is only a slow and moderate variation in frequency, whereas in *subflava* it varies sharply and extensively—the notes of *fluviatilis* never show on a sonagram the fine striations (due to frequency modulation) produced by *subflava* (Fig. 4). These vocal characteristics are recognisable in the field and in addition the habitats of the 2 prinias are specifically distinct. Subtle but definite morphological differences have also been revealed.

ORANGE-THROATED APALIS spp.: **GOSLING'S APALIS** *Apalis goslingi*, **BAMENDA APALIS** *A. bamendae*, **BUFF-THROATED APALIS** *A. rufogularis* and **SHARPE'S APALIS** *A. sharpii* (Chappuis 1974–85, Chappuis 1980)

Acoustical analysis was used to separate a member of this group, the Chestnut-throated Apalis *A. porphyrolaema*, from others (Keith & Gunn 1971). The above 4 *Apalis*, which were given specific status by Bannerman (1953) and by Mackworth-Praed & Grant (1970), were treated by White (1960) as *A. rufogularis, A. sh. sharpii, A. sharpii bamendae* and *A. sharpii goslingi*. White's arrangement is not supported by these forms' vocal structure: *rufogularis* and *sh. sharpii* utilize a repertoire of structurally similar motifs (with positive reactions to each other's playback in the field) and must be treated as a superspecies. *goslingi* and *bamendae* utilize a repertoire of simple notes, of strongly modulated frequency in *bamendae*, but little modulated and of a more rapid tempo in *goslingi* (Fig. 6). The latter are 2 distinct species that live in very different habitats.

JAMBANDU INDIGOBIRD *Vidua raricola* (Payne 1982)

Male *raricola* mimic the song of the Black-bellied Fire-finch *Lagonosticta rara* and the young indigobirds mimic the latter's mouth pattern (gape tubercles and spots on the roof of the mouth). The distribution of *V. raricola* matches closely that of *L. rara* (see later discussion). They are both found in Sierra Leone, Ghana and northern Cameroun. (See Vuilleumier *et al.* this volume.)

BAKA INDIGOBIRD *Vidua larvaticola* (Payne 1982)

Parasitizes and mimics vocally the Black-faced Fire-finch *Lagonosticta larvata*. *V. larvaticola* is distinguished by the same adaptations to its host as those of *V. raricola* (see later discussion). It ranges from Senegambia to Ethiopia. (See Vuilleumier *et al.* this volume.)

Discussion

The above examples are given in a plea to restore the importance of avian taxonomic research, at present so severely neglected in several countries, emphasised by the drastic reduction in funds apportioned to museums. Denial of research amounts to a threat to the collections which are the foundations of these museums. This disfavour has several causes. Taxonomic research has become overshadowed by the great impulse of more recent disciplines, such as ecology and ethology; in comparison taxonomy is wrongly coming to be considered an outdated discipline. In addition, a frequently uncritical regard for life demands preclusion of the killing of any bird whatever for whatever reasons, enhanced by unconfirmed opinion that museums are well stocked with specimens and that collecting is a direct unmeasured threat to uncommon species. Nevertheless, knowledge and documentation of many species is markedly insufficient for their own conservation, particularly in West Africa, whereas the insatiable thirst of some past collectors no longer exists. Many species are considererd endangered on account of their small populations, while knowledge of their taxonomic status as well as of their degree of genetic isolation is possibly essential for their protection and even their survival.

The new species cited are examples of many others that have required or require taxonomy to resolve their problems. The Spoonbill *Platalea leucorodia* and the Little Bittern *Ixobrychus minutus* breed in the Senegal valley, i.e. within the tropics. The Spoonbill has not been collected, so its taxonomic status or whether it is endemic and requires especial protection is unknown; the Little Bittern is thought to be of the nominate race, but this needs confirmation (Morel & Morel 1989). The Glossy Ibis *Plegadis falcinellus* that was nesting in northern Mali (Morel & Morel 1966) was not observed again and its taxonomic status also remains unknown. In the contact zone of the western (*savilei*) and of the eastern (*gindiana*) African Crested Bustard *Eupodotis ruficrista* the question whether the 2 populations are vocally isolated deserves study. The chance discovery of other new species undoubtedly awaits the knowledgeable explorer, but this will happen more and more rarely.

Taxonomy, however, is receiving fresh impulse from modern techniques with live birds. Mathematical aid (e.g. discriminant analysis) can be instrumental in morphological studies (wing, tail and tarsus length) of outwardly similar forms, e.g. *Cisticola dorsti* and subspecies of *C. ruficeps* (Chappuis & Erard 1991). Also, when only tiny fragments of feather or very small samples of blood are available, DNA analysis can help to distinguish allied forms, as was the case in describing *Laniarius liberatus* (Smith *et al.* 1991) in Somalia, where one live specimen only could be secured, and had to be released. (See also Vuilleumier *et al.* this volume.)

About half of the new forms mentioned above from West Africa clearly indicate that bioacoustics (supported by biometrics) was the decisive technique used in their discovery (*Prinia fluviatilis, Vidua* spp.) or in elucidating their superspecies status (*Otus scops, Cuculus canorus* . . .). Bioacoustics is relevant in 2 types of problem. Firstly, with populations in sympatry: no two sympatric populations with distinct vocalizations can be from a single species, more especially if these vocalizations can be correlated with distinct habitats. Secondly, it is relevant with allopatric populations, when assessment is more delicate and is based on the importance of the acoustical deviation in the following main parameters: range of notes, their speed of frequency variation, and the harmonic and temporal structure of the call or song. These differences, of course, will be all the more significant if they concern several of these parameters simultaneously (Chappuis 1980). The value of vocalizations as a means of distinguishing forms is now recognized, and the diagnosis of every new species should generally include a paragraph on 'Voice' with sonagrams.

Finally, the outstanding study of Payne (1982) on the genus *Vidua* deserves mentioning. The confusing black plumage of all *Vidua* (=

Hypochera) males, more or less greenish or bluish depending on the light, had always been a challenge to taxonomists. Amongst other parasitic avian species, the specific adaptation of the nestling's mouth marks to that of the host, as shown by Payne, is unique. The number of queried synonyms and the *nomina dubia* still left unresolved attests to the difficulty of the task and is also a stimulating invitation for further research, including especially the vocalisation differences and mimicry of the male *Vidua*.

Acknowledgements

We express our thanks to J. H. Elgood over *M. ibadanensis* and to J. F. Monk for improving our text and our English.

References:

Bannerman, D. A. 1949. *The Birds of Tropical West Africa*. Vol. 7. London, Crown Agents.

— 1953. *The Birds of West and Equatorial Africa* 2 vols. Oliver & Boyd.

Bannerman, D. A,. & Bannerman, W. M. 1968. *History of the Birds of The Cape Verde Islands*. Oliver & Boyd.

Brown, L. E., Urban, E. K. & Newman, K. 1982. *The Birds of Africa*. Vol. 1. Academic Press.

Chappuis, C. 1974–1985. Illustration sonore de problèmes bioacoustiques posés par les oiseaux de la zone éthiopienne. *Alauda* 42: 197–222 & 467–500, 46: 327–355, 47: 192–212; with accompanying discs. Soc. Etudes Orn. Muséum, 4, avenue du Petit-Château. 91800 Brunoy, France.

— 1980. Study and analysis of certain vocalizations as an aid in classifying African Sylviidae. *Proc. IV Pan-Afr. Orn. Congr. 1976:* 57–63.

Chappuis, C. & Erard, C. 1973. A new race of Pectoral-patch Cisticola from Cameroun. *Bull. Brit. Orn. Cl.* 93: 143–144.

—, — 1991. A new cisticola from west-central Africa. *Bull. Brit. Orn. Cl.* 111: 59–70.

Chappuis, C., Erard, C. & Morel, G. J., 1979. Données comparatives sur la morphologie et les vocalisations des diverses formes d'*Eupodotis ruficrista*. *Malimbus* 1: 74–89.

—, —, — (in press). Morphology, habitat, vocalizations and distribution of the River Prinia *Prinia fluviatilis* Chappuis. *Proc. VII Pan-Afr. Cong.*

Collar, N. J. & Stuart, S. N. 1985. *Threatened Birds of Tropical West Africa*. 3rd Edn. Part 1. ICBP/IUCN Red Data Book. ICBP.

Colston, P. R. 1981. A newly described species of *Melignomon* (Indicatoridae) from Liberia, West Africa. *Bull. Brit. Orn. Cl.* 101: 289–291.

Colston, P. R. & Curry-Lindahl, K. 1986. *The Birds of Mount Nimba, Liberia*. British Museum (Natural History), London.

Colston, P. R. & Morel, G. J. 1984. A new subspecies of the African Reed Warbler *Acrocephalus baeticatus* from Senegal. *Bull. Brit. Orn. Cl.* 104: 3–5.

—, — 1985. A new subspecies of the Rufous Swamp Warbler *Acrocephalus rufescens* from Senegal. *Malimbus* 7: 61–62.

Eisentraut, M. 1963. *Die Wirbeltiere des Kamerungebirges*. Hamburg & Berlin.

Elgood, J. H. 1958. A new species of *Malimbus*. *Ibis* 100: 621–624.

— 1988. Rediscovery of *Malimbus ibadanensis* Elgood, 1958. *Bull. Brit. Orn. Cl.* 108(4): 184–185.

Erard, C. 1991. Variation géographique de *Bleda canicapilla* (Hartlaub) 1854 (Aves, Pycnonotidae). Description d'une sous-espèce nouvelle en Sénégambie. *L'Oiseau et R.F.O.* 61: 66–67.

Erard, C. & Roux, F. 1983. La Chevêchette du Cap *Glaucidium capense* dans l'Ouest africain. Description d'une race géographique nouvelle. *L'Oiseau et R.F.O.* 53: 97–104.

Forbes-Watson, A. D. 1970. A new species of *Melaenornis* (Muscicapinae) from Liberia. *Bull. Brit. Orn. Cl.* 90: 145–148.

Fry, C. H., Keith, S. & Urban, E. K. 1988. *The Birds of Africa*. Vol 3. Academic Press.

Gatter, W. 1985. Ein neuer Bülbül aus Westafrika (Aves, Pycnonotidae). *Journal f. Orn.* 126: 155–161.

Giraudoux, P., Degauquier, R., Jones, P. J., Weigel, J. & Isenmann, P. 1988. Avifaune du Niger: état des connaissances en 1986. *Malimbus* 10: 1–140.

Grimes, L. G. 1987. *The Birds of Ghana*. British Ornithologists' Union, Tring, UK.

Heim de Balsac, H. & Mayaud, N. 1962. *Les Oiseaux du Nord-ouest de l'Afrique.* P. Lechevalier, Paris.

Howard, R. & Moore, A. 1980. *A Complete Check-list of the Birds of the World.* Oxford University Press.

Jouanin, C. & Roux, F. 1963. Une race nouvelle de Héron cendré *Ardea cinerea monicae. L'Oiseau et R.F.O.* 33: 103–106.

Keith, S. & Gunn, W. W. H. 1971. Birds of African Rain Forests. *Sounds of Nature* No. 9. Federation of Ontario Naturalists, Don Mills Ontario (two 12 inch discs).

Lamarche, B. 1980–1981. Liste commentée des oiseaux du Mali. *Malimbus* 1: 121–158; 2: 73–102.

— 1988. Liste commentée des oiseaux de Mauritanie. *Etudes sahariennes et ouest-africaines.* 1, 4 et spécial.

Louette, M. 1981. A new species of Honeyguide from West Africa (Aves, Indicatoridae). *Revue Zool. Afr.* 95: 131–135.

Mackworth-Praed, C. W. & Grant, C. H. B. 1970. *Birds of West Central and Western Africa. African Handbook of Birds.* Series 3, Vol. 1. Longman.

Mahé, E. 1985. Contribution à l'étude scientifique de la région de Banc d'Arguin. 21°20′N/19°20′N. Peuplements avifaunistiques. 2 fascicules. *Thèse Acad.* Montpellier. 575 pp and 56 pp.

Morel, G. J. & Morel, M-Y. 1989. Une héronnière mixte sur le lac de Guier (Sénégal) avec référence spéciale à *Ixobrychus m. minutus* et *Platalea leucorodia. L'Oiseau et R.F.O.* 59: 290–295.

Morel, G. J. & Roux, F. 1962. Données nouvelles sur l'avifaune du Sénégal. *L'Oiseau et R.F.O.* 32: 28–56.

—, — 1966. Les migrateurs paléarctiques au Sénégal. *Terre et Vie* 20. 1. Non-passereaux: 19–72; Passereaux et synthèse générale: 143–176.

Naurois, R. de. 1966. Le Héron pourpré de l'archipel du Cap Vert, *Ardea purpurea bournei* ssp. nov. *L'Oiseau et R.F.O.* 36: 89–94.

Naurois, R. de & Roux, F. 1974. Précisions concernant la morphologie, les affinités et la position systématique de quelques oiseaux du Banc d'Arguin (Mauritanie). *L'Oiseau et R.F.O.* 44: 72–84.

Payne, R. B. 1977. Juvenile plumage of *Cuculus canorus* and *Cuculus gularis* in Africa. *Bull. Brit. Orn. Cl.* 97: 48–54.

— 1982. *Species Limits in the Indigobirds* (Ploceidae, *Vidua*) *of West Africa: Mouth Mimicry, Song Mimicry, and Description* of *New Species.* Museum of Zoology, University of Michigan, No 162. Ann Arbor.

Serle, W. 1959. Note on the immature plumage of the Honey-guide *Melignomon zinkeri* Reichenow. *Bull. Brit. Orn. Cl.* 79: 65.

Smith, E. F. G., Arctander, P., Fjeldså, J. & Amir, O. G. 1991. A new species of shrike (Laniidae: *Laniarius*) from Somalia, verified by DNA sequence data from the only known individual. *Ibis* 133: 227–235.

Snow, D. W. 1978. *An Atlas of Speciation in African Non-Passerine Birds.* British Museum (Natural History), London.

Urban, E., Fry, C. H. & Keith, S. 1986. *The Birds of Africa.* Vol. 2. Academic Press.

Van der Weyden, W. J. 1973. Vocal affinities of the African and European Scops Owls *Otus scops* (Strigidae). *Bull. IFAN.* 35 sér. A, No. 3: 716–722.

White, C. M. N. 1960. A Check List of the Ethiopian Muscicapidae (Sylviinae). Part 1. *Occ. Pap. Nat. Mus. Southern Rhodesia*: 704–707.

— 1965. *A Revised Check List of African Non-Passerine Birds.* Government Printer, Lusaka.

Addresses: Dr Gérard J. Morel, 1, route de Sallenelles, 14860 Bréville-les-Monts, France.
Dr Claude Chappuis, "Les Chardonnerets", Lotissement du Fer à Cheval, La Bouille, 76530 Grand-Couronne, France.

© British Ornithologists' Club 1992

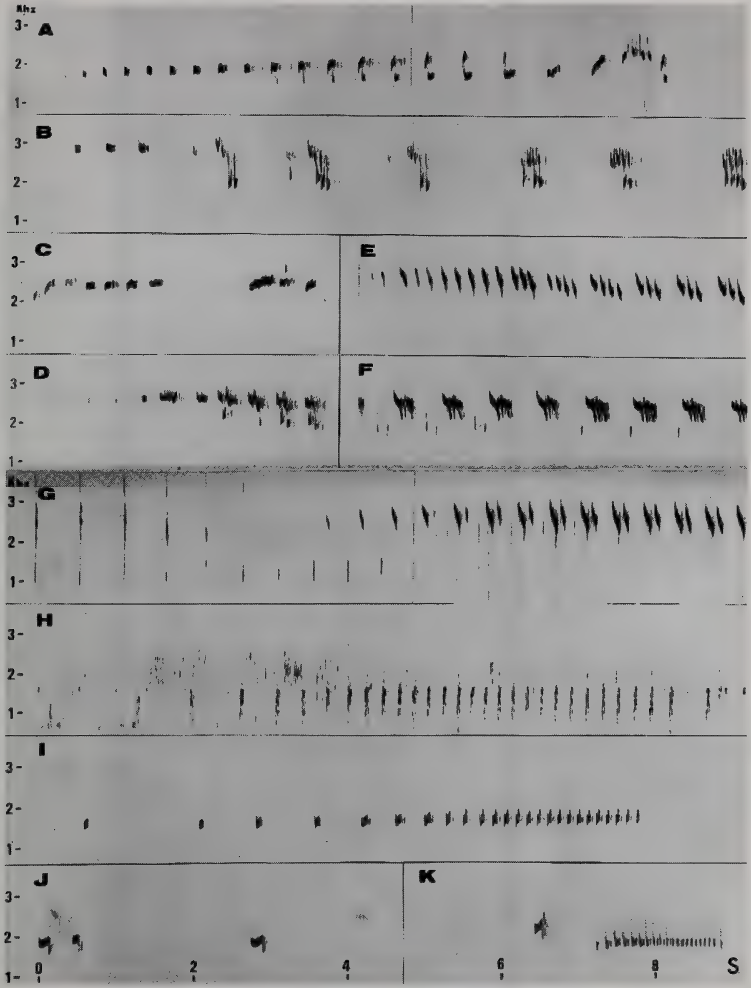


Figure 1. Sonagrams (analysed in wide band, 300 hz) of *Eupodotis* species. Frequencies in Khz, time in sec. A–D: *gindiana*. A = song of ♀, B = segment of song of ♂, C = immature, D = short phrase of ♂. E–G: *ruficrista* = parts of song. H–K: *savilei*. H = song (of immature ?), I and K = song of adults, J = call note. In *gindiana* and *ruficrista* the structural similarity of notes and motifs in D, E, F and G support the opinion that they are conspecific: the phrase begins with a note which progressively turns into a motif. The rhythm shows no acceleration. In *savilei* the initial note remains unchanged throughout the phrase but the rhythm increases progressively.

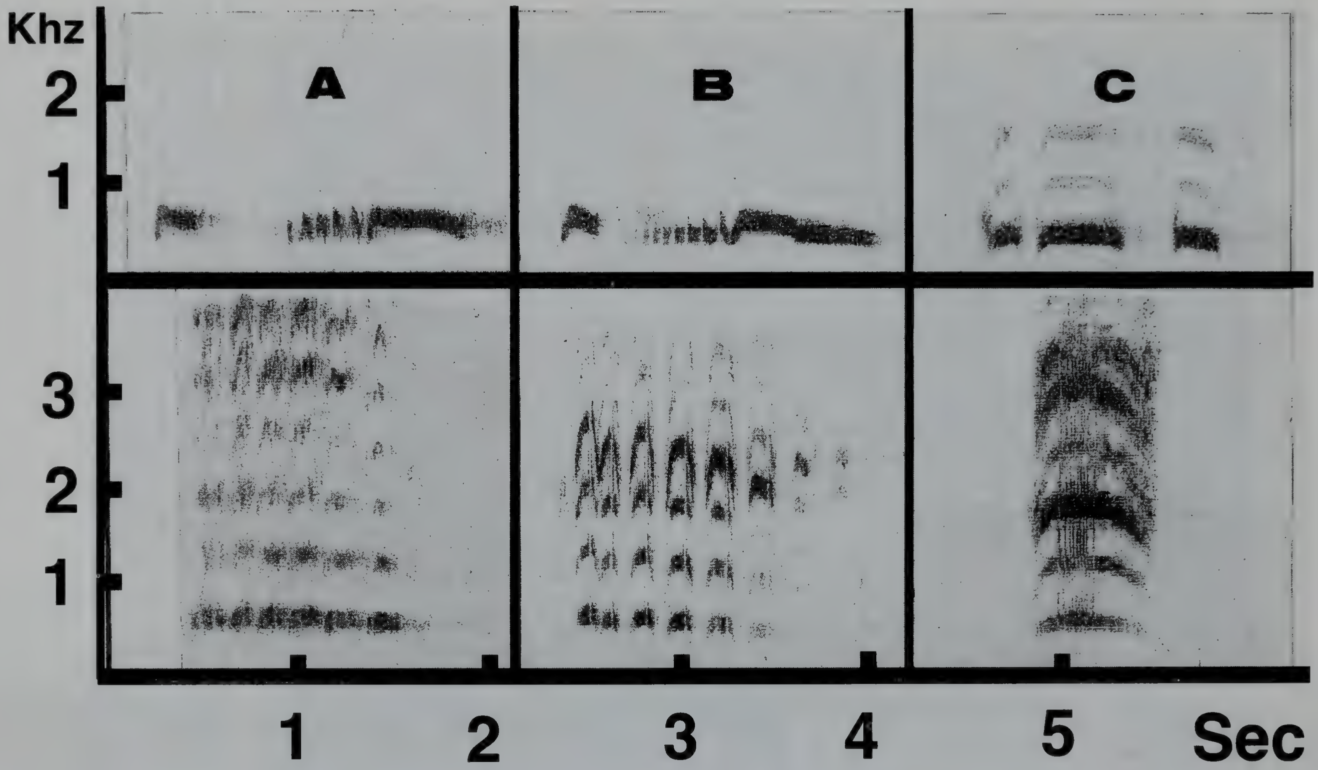


Figure 2. Sonagrams of *Streptopelia roseogrisea* (domesticated form), *roseogrisea* (wild, Mali), *decaocto* (France). Top = song, bottom = cry. Similarity of calls of *roseogrisea* A (domesticated) and (wild) (= B) should be noted and their striking difference from *decaocto*'s.

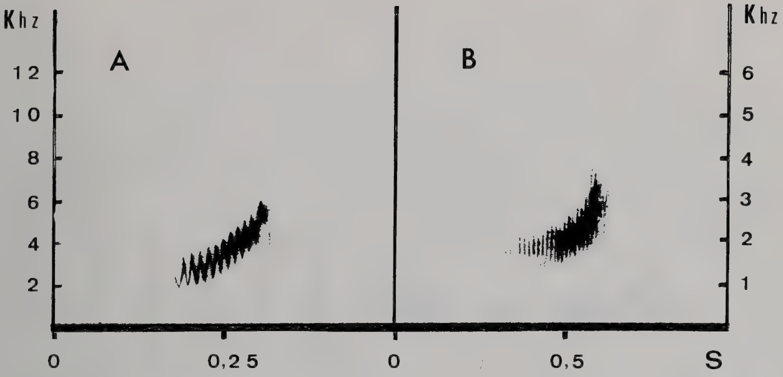


Figure 3. Comparison of an isolated call in 2 *Stizhorina* (each analysed on a different scale). A=*fraseri*, on a frequency scale of 0–16 Khz; duration of cry c. 0.135 secs. B=*finschi*, on a scale of 0–8 Khz, but with a doubled time scale; duration of cry c. 0.35 secs, i.e. more than double that of *fraseri*.

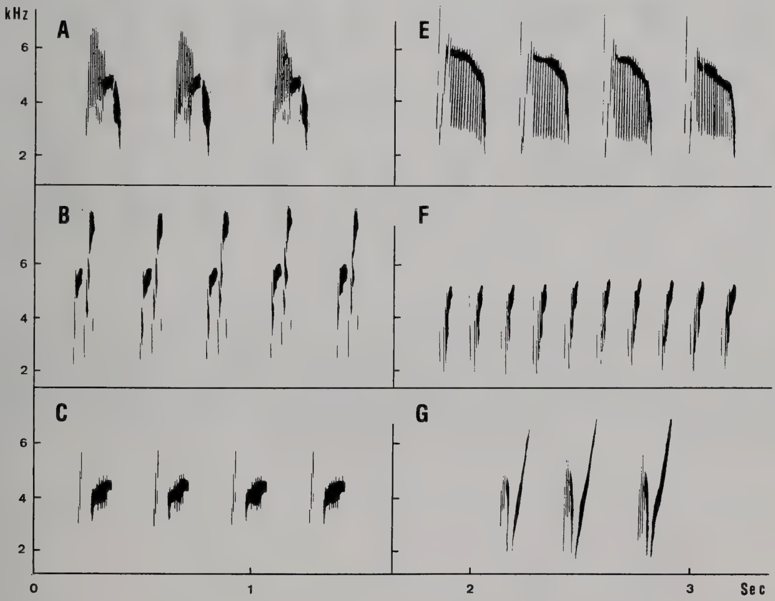


Figure 4. Song of *Prinia subflava* from western and eastern Africa. A, B, C from Nigeria. E, F, G from Kenya. The fast rhythm of F indicates territorial flight song. The fine striations of notes, a specific character, are not always visible on sonagram copies.

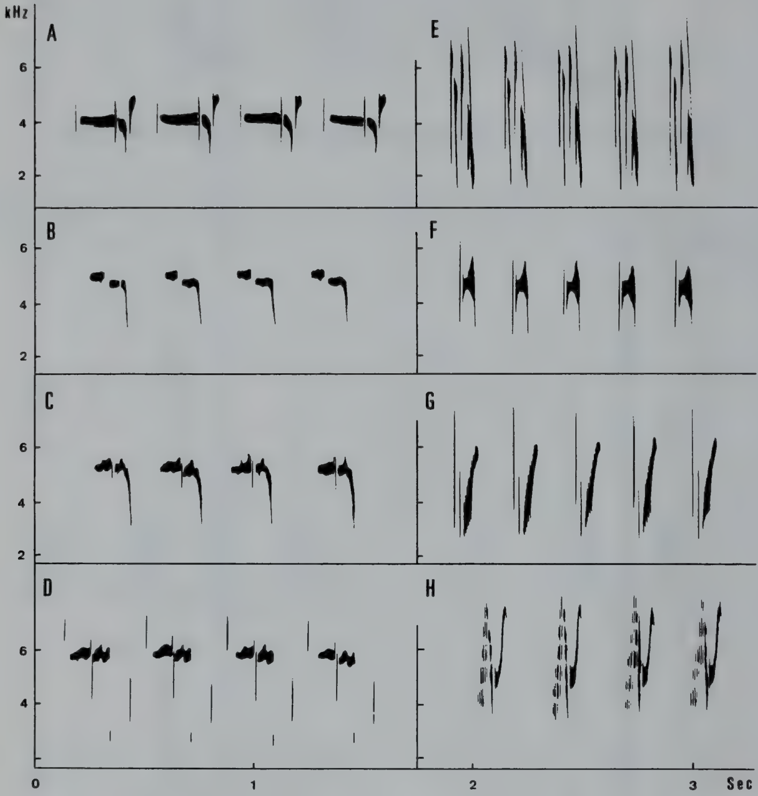


Figure 5. Song comparison of *Prinia fluviatilis* and *P. subflava: fluviatilis* = A (Chad), B (Niger), C and D (NW Senegal); *subflava* = E (Kenya), F and G (Chad), H (N Senegal). In *subflava* the main volume is delivered on one note, with fast variations of frequency on a broad segment; in *fluviatilis* this variation is small and slow.

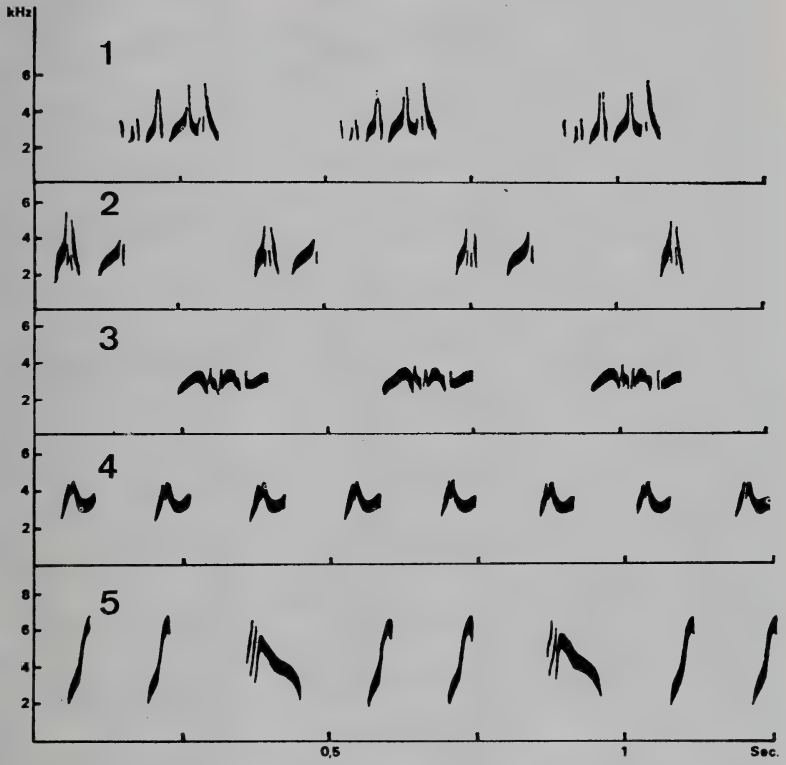


Figure 6. Songs of 4 Apalis males (frequency scale from 160 to 16,000 Hz). 1 = *rufogularis*, S. Cameroun; 2 and 3 = *sharpii*, Ivory Coast; 4 = *goslingi*, Gabon; 5 = *bamendae*, S. W. Cameroun. Two groups of rhythm appear: (1) 4–6 notes per second: *A. goslingi* and *A. bamendae*. These 2 species differ from each other by the scale of variation of frequencies. (2) 2.5–3.2 motifs per second: *A. rufogularis* and *A. sharpii*, which present considerable similarity in the structure of the notes and the motifs.

TABLE 1

Summary of species included in the genus *Sporophila* by various authors: A = Ridgely & Tudor (1989); B = Morony, Bock & Farrand (1975); C = Paynter & Storer (1970); D = Sibley & Monroe (1990); E = Meyer de Schauensee (1952); F = Wolters (1980); G = Hellmayr (1938). The asterisk (*) indicates a species listed by a given author.

Sporophila	A	B	C	D	E	F	G
1. *lineola*	*	*	*	*	*	*	*
2. *bouvronides*	*	—	—	*[1]	—	—	*
3. *americana*	*	*	*	*	*	*	*
4. *collaris*	*	*	*	*	*	*	*
5. *nigricollis*	*	*	*	*	*	*	*
6. *ardesiaca*	*	*	*	*	—	*	—[2]
7. *melanops*	*	*	*	*	*	*	*
8. *luctuosa*	*	*	*	*	*	*	*
9. *caerulescens*	*	*	*	*	*	*	*
10. *peruviana*	*	*	*	*	*	*	—
11. *albogularis*	*	*	*	*	*	*	*
12. *frontalis*	*	*	*	*	*	*	*
13. *schistacea*	*	*	*	*	*	*	*
14. *intermedia*	*	*	*	*	*	*	*
15. *falcirostris*	*	*	*	*	*	*	*
16. *plumbea*	*	*	*	*	*	*	*
17. *simplex*	*	*	*	*	*	*	*
18. *leucoptera*	*	*	*	*	*	*	*
19. *telasco*	*	*	*	*	*	*	*
20. *insulata*	*	*	*	*	*	*	*
21. *bouvreuil*	*	*	*	*	*	*	*
22. *hypoxantha*	*	*	*	*[3]	—	*	—[4]
23. *minuta*	*	*	*	*	*	*	*
24. *hypochroma*	*	*	*	*[5]	—	*	*
25. *nigrorufa*	*	*	*	*	*	*	*
26. *melanogaster*	*	*	*	*	*	*	*
27. *castaneiventris*	*	*	*	*	*	*	*
28. *cinnamomea*	*	*	*	*	*	*	*
29. *palustris*	*	*	*	*	*	*	*
30. *ruficollis*	*	*	*	*	*	—	*
31. *zelichi*[6]	*	—	—	*	—	—	—
32. *torqueola*	—[7]	*	*	*	*	*	*
33. *obscura*	—[8]	*	*	—	*	*	*
34. *aurita*	—	—	—	—	—	—	*[9]
35. *lorenzi*	—	—	—	—	—	—	*[10]
36. *saturata*	—	—	—	—	—	—	*[11]
Number of species	31	31	31	32	28	30	32

[1] allospecies of *lineola*.
[2] a subspecies of *nigricollis*.
[3] allospecies of *minuta*.
[4] a subspecies of *minuta*.
[5] allospecies of *cinnamomea*.
[6] described in 1977 (see Narosky 1977).
[7] not in the range of the work of these authors.
[8] placed in genus *Tiaris* by these authors.
[9] cf. *americana*
[10] cf. *palustris*.
[11] cf. *bouvreuil*.

S. torqueola included. The taxa, as listed by each author, are summarized in Table 1.

The status of *S. bouvronides* has fluctuated between that of a subspecies of *S. lineola* (Meyer de Schauensee 1952, Paynter & Storer 1970, Morony *et al.* 1975, Wolters 1980) to that of a species (Hellmayr 1938, Schwartz 1975, Ridgely & Tudor 1989), and more recently as an allospecies of *S. lineola* (Sibley & Monroe 1990); but the relationship of *bouvronides* and *lineola* remains unclear. Hellmayr (1938), on the other hand, had treated *S. ardesiaca* as a subspecies of *S. lineola,* although it is presently recognized as a species by most authors; but Meyer de Schauensee (1952) did not include it in his revision and it may prove to be a hybrid (Sick 1962, 1963).

Hellmayr (1938) placed *S. peruviana* in the genus *Neorhynchus* which was considered later to be congeneric with *Sporophila* (Meyer de Schauensee 1952).

Hellmayr (1938) listed *S. hypoxantha* as a subspecies of *S. minuta.* Meyer de Schauensee (1952) considered *S. hypoxantha* to be conspecific with *S. minuta*, and *S. hypochroma* with *S. castaneiventris*. Wolters (1980) on the other hand regarded *S. ruficollis* as conspecific with *S. hypoxantha.* Most recently Sibley & Monroe (1990) consider *S. hypoxantha* to be an allospecies of *S. minuta*, and *S. hypochroma* to be an allospecies of *S. cinnamomea.*

S. zelichi was not described until 1977 (Narosky 1977) and was consequently included only in classifications published after that date.

S. obscura has been classified until recently in the genus *Sporophila* by most authors, but has been transferred latterly to the genus *Tiaris* (Ridgely & Tudor 1989, Sibley & Monroe 1990) on the basis of earlier recommendations (Collins & Kemp 1976, Clark 1986). *S. aurita, lorenzi* and *saturata*, valid species in Hellmayr (1938), were synonymized respectively as *S. americana, palustris* and *bouvreuil* by other authors (Table 1).

Olson (1981a), in reviewing characters of the genus *Oryzoborus*, considered the shape of the bill to have little taxonomic value at the generic level and recommended that *Oryzoborus* be considered congeneric with *Sporophila.* This recommendation has not been followed so far, but, should it be adopted, the genus *Sporophila* would thus include 5 additional species: *Oryzoborus nuttingi*, *crassirostris*, *atrirostris*, *maximiliani* and *angolensis*, as listed in recent works (Ridgely & Tudor 1989, Sibley & Monroe 1990).

Colours and colouration patterns

Ridgely & Tudor (1989) divided the genus *Sporophila* into 7 distinct groups based on plumage colouration and patterns, an arrangement apparently designed primarily for field identification purposes and not essentially for taxonomic reasons. In Fig. 1, for taxonomic purposes I have divided the species of the genus *Sporophila*, including *obscura*, into plumage types based on the affinities of colour or colouration patterns in males; they show the extensive variation in colours or colouration patterns found in the genus and represent 5 distinct groups. This approach is highly artificial, but allows the grouping of species into smaller more meaningful units for comparative purposes. Although I am uncertain about the value of such an approach, it clearly indicates external character affinities between groups and the members of groups, or even between the genus *Sporophila* and other closely related genera.

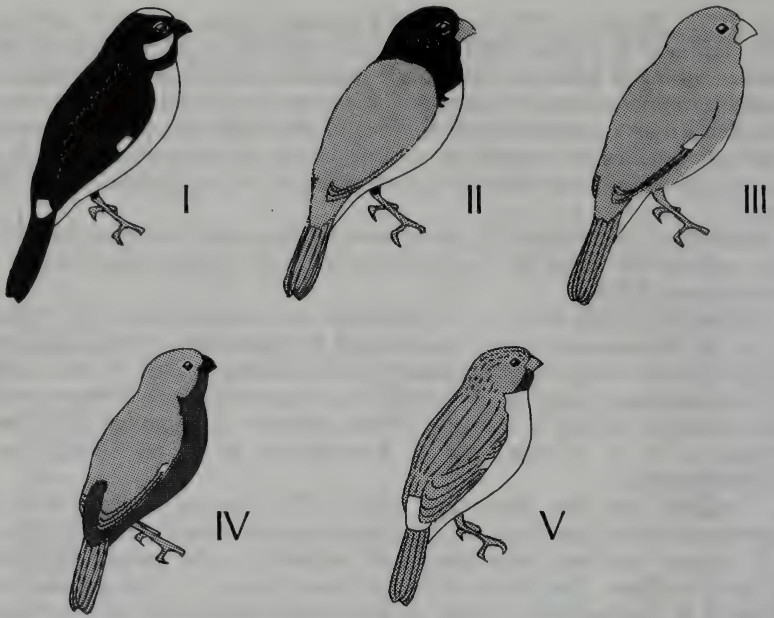


Figure 1. The genus *Sporophila*, separated into 5 groups (Types) based on the colour or colouration patterns of males. Each 'Type' depicts a typical species, followed by the other species assigned to this group. **Type I**. Mostly black and white or buff: *lineola—bouvronides*, *americana* (including *aurita*), *collaris* and *torqueola*. **Type II**. Black facial mask or hood: *nigricollis—ardesiaca*, *melanops*, *luctuosa* and *obscura* (*Tiaris*). **Type III**. Uniform grey or buff upper parts: *intermedia—caerulescens*, *peruviana*, *albogularis*, *schistacea*, *plumbea*, *falcirostris*, *leucoptera*, *frontalis* and *simplex*. **Type IV**. Cinnamon, chestnut or rusty under parts: *minuta—bouvreuil*, *hypoxantha*, *hypochroma*, *nigrorufa*, *castaneiventris*, *cinnamomea*, *palustris*, *ruficollis*, *zelechi* and *melanogaster* (black under parts). **Type V**. Streaked upper parts and white at base of tail: *telasco—insulata*. The illustrations were prepared by Michel Gosselin.

Plumage and colouration patterns are highly variable in some members of the genus, as illustrated by the extensive geographic variation reported in 2 well studied species: *S. torqueola* (Monroe 1968, Meyer de Schauensee 1952) and *S. americana* (Olson 1981b, Meyer de Schauensee 1952). I have placed *S. [Tiaris] obscura* in Type II and *S. simplex* in Type III, although the colouration of these birds does not suggest straightaway such an arrangement because the dominant colour appears to conceal a less obvious colouration pattern. The principal merit of this arbitrary arrangement is to assemble into homogeneous groups species that appear to share several external morphological features.

Size

Seedeaters are in general small and never attain the large body dimensions of many Emberizines. Using wing length as a general indicator of body size, wings (chord) range from 52 to 66 mm in males, the females being slightly smaller. The bill (exposed culmen) of males varies

TABLE 2

Measurements, in mm, for wing chord and exposed culmen of species in the genus *Sporophila*. Numbers in parentheses show the sample size and are followed by the mean and standard deviation of the mean. Numbers in square brackets indicate data obtained from Meyer de Schauensee (1952), Hellmayr (1938) and Short (1969).

	Sporophila	Wing (chord)	Culmen (exposed)
1.	*lineola*[1]	(39) 58.2±1.99	(37) 7.4±0.38
2.	*bouvronides*	(37) 53.7±2.11	(37) 7.6±0.28
3.	*americana*[2]	(14) 57.4±1.66	(14) 9.9±0.53
4.	*collaris*	[56–59]	—
5.	*nigricollis*	(26) 55.3±1.99	(26) 8.2±0.37
6.	*ardesiaca*	[60]	—
7.	*melanops*	[55]	[8]
8.	*luctuosa*	(25) 56.7±1.29	(25) 8.1±0.51
9.	*caerulescens*	(23) 57.4±1.44	(23) 8.5±0.46
10.	*peruviana*	[56–59]	[14–15]
11.	*albogularis*	[65]	—
12.	*frontalis*	[65–68]	[12–13]
13.	*schistacea*[3]	(15) 62.0±0.72	(15) 9.8±0.32
14.	*intermedia*[4]	(49) 56.6±2.19	(49) 9.9±0.44
15.	*falcirostris*	(1) 54.8	(1) 10.7
16.	*plumbea*[5]	(26) 58.1±1.28	(26) 9.2±0.47
17.	*simplex*	(1) 59.9	(1) 10.2
18.	*leucoptera*	(6) 61.2±2.2	(6) 11.2±1.02
19.	*telasco*	(10) 53.1±0.97	(9) 8.2±0.35
20.	*insulata*	[50]	[9.3]
21.	*bouvreuil*	(1) 54.5	(2) 7.9
22.	*hypoxantha*	[52.6–55.6]	[5.6–6.5]
23.	*minuta*[6]	(24) 50.8±1.63	(22) 7.9±0.36
24.	*hypochroma*	[50.9–53.9]	[5.7–6.2]
25.	*nigrorufa*	(2) 50.6	(2) 7.7
26.	*melanogaster*	[55–56]	[9]
27.	*castaneiventris*	(12) 49.6±1.46	(10) 7.6±0.52
28.	*cinnamomea*	[56.5]	[9]
29.	*palustris*	(2) 53.6	(2) 8.1
30.	*ruficollis*	(2) 50.9	(2) 8.0
31.	*zelichi*	[54–55]	[8]
32.	*torqueola*[7]	(13) 51.9±1.5	(13) 8.4±0.51
33.	*obscura*[8]	(22) 55.4±1.7	(20) 8.8±0.81

[1] *S.l.lineola.*
[2] *S.a.americana.*
[3] *S.s.schistacea.*
[4] *S.i.intermedia.*
[5] *S.p.whiteleyana.*
[6] *S.m.minuta.*
[7] *S.t.morelleti.*
[8] *S.o.obscura.*

from 5.6 to 13.0 (15?)mm (Table 2), females again being somewhat smaller. It is interesting to note that nearly all the larger species generally belong to Type I (Fig. 1), that the smaller ones fall in Type II, and that the species of intermediate size are distributed among the other 3 plumage types. Although species with a more brightly coloured plumage appear more frequently to have smaller body dimensions, this correlation may be purely coincidental and appears to have no adaptive or evolutionary significance.

Sexual dimorphism

Sexual plumage dimorphism is well marked in the genus *Sporophila*, the males of most species having a conspicuously more colourful or contrasting plumage in comparison with the dull beige female plumage. However, intersexual plumage differences are slight in a few species, such as *obscura*, *simplex* and *frontalis*. The drab female plumages, generally without obvious distinctive traits, make species identification often difficult or impossible even for some birds in the hand. Sexual size dimorphism is less noticeable, but females have in general smaller (±15%) body dimensions, with wing and tail lengths showing most difference and tarsus and culmen lengths least.

SPECIATION

In Table 3 I have listed the monotypic and polytypic species of the genus *Sporophila*. Nineteen species are monotypic and show so little geographic variation that no subspecies is currently recognized in any of them. Fourteen species are polytypic with 2 or more accepted subspecies, although the taxonomic status of some of them is dubious pending reviews of their status based on new material. The extent of individual and geographic variation, as well as the characteristics and distribution of many subspecies, remain incompletely studied. Detailed revisions are now necessary to understand clearly the evolution of this group, because most of the work on this aspect has been done at a time when less extensive

TABLE 3

List of monotypic and polytypic species in the genus *Sporophila*. Numbers in parentheses show the number of currently recognized subspecies.

Sporophila Monotypic species [19]	*Sporophila* Polytypic species [14]
bouvronides	*lineola* (2)
ardesiaca	*americana* (7)
melanops	*collaris* (3)
luctuosa	*nigricollis* (3)
albogularis	*caerulescens* (3)
frontalis	*peruviana* (2)
falcirostris	*schistacea* (4)
simplex	*intermedia* (4)
telasco	*plumbea* (3)
insulata	*leucoptera* (4)
hypoxantha	*bouvreuil* (4)
hypochroma	*minuta* (3)
nigrorufa	*torqueola* (5)
melanogaster	*obscura* (4)
castaneiventris	
cinnamomea	
palustris	
ruficollis	
zelichi	

material was available than it is now and when the criteria for subspecific recognition were different.

The problems resulting from intergeneric and interspecific hybridization have been recognized for some time (Lordello 1957, Sick 1963) but have not been studied or assessed adequately in many instances. Consequently, the validity or the relationships of several taxa, especially *S. hypoxantha*, *hypochroma*, *insulata*, *palustris*, *zelichi*, *lineola* and *bouvronides*, remain in doubt. The access to new information and material and the use of new techniques should foster a fresh understanding of geographic variation and permit a critical evaluation of the status of subspecies, as well as interspecific and intergeneric relationships.

ZOOGEOGRAPHY

General distribution

The genus *Sporophila* is primarily a South American taxon, but representative species occur on both sides of the equator from southern Texas (Rio Grande Valley) in the United States (*S. torqueola*) (American Ornithologists' Union 1983) through Central America south to southern Argentina (*S. caerulescens* and *S. ruficollis*) (Paynter & Storer 1970, Ridgely & Tudor 1989, Sibley & Monroe 1990). Species diversity is least at the northern and southern extremities of the range of the genus and attains its maximum between 10°N and 30°S (Fig. 2). This area forms a vast and ecologically diversified continental region with a complex evolution and history (Haffer 1985, 1987) in which the distribution and evolution of the genus *Sporophila* remain uninterpreted. Few of its species have colonized islands (Meyer de Schauensee 1952) and only one,

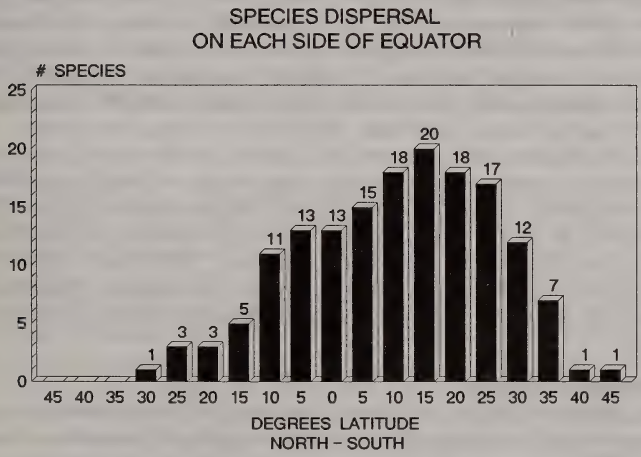


Figure 2. Diagram showing the number of species in the genus *Sporophila* recorded at various latitudes, north and south of the equator, compiled from the sources listed in Table 1. The number at the top of each bar represents the number of species occurring in a band of 5° latitude.

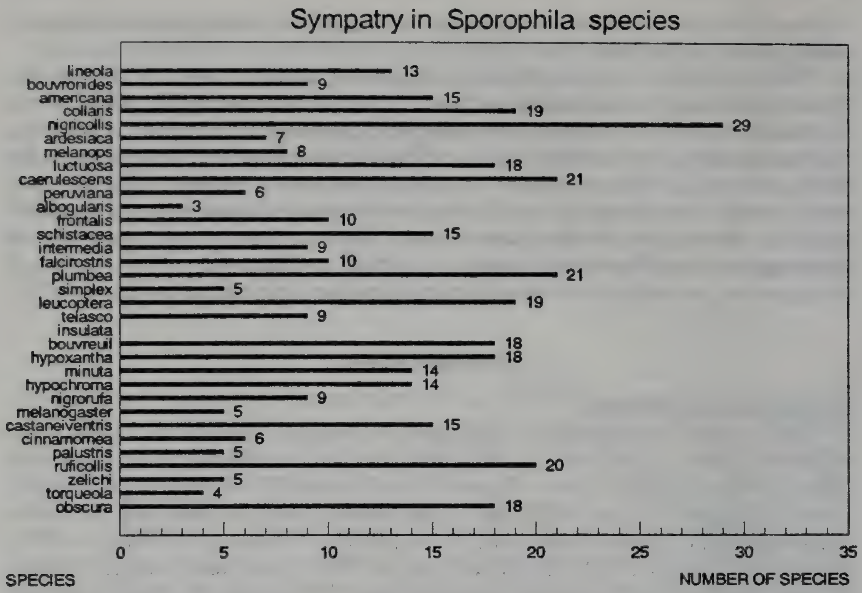


Figure 3. Diagram showing the species of the genus *Sporophila* and the number of species with which each species is sympatric.

S. insulata, has been found to be endemic and either allopatric or parapatric pending a review of its taxonomic status.

Sympatric species

All *Sporophila* species, with the exception of *insulata*, are sympatric with 3 or more congeners (Fig. 3). The totals in Fig. 3 are based on the number of taxa with which a given species is sympatric in any part of its range, even in a small portion of it. Most species are sympatric with less than 10 congeners, and only a few with a large number of congeners. *S. nigricollis*, *caerulescens*, *plumbea*, *ruficollis*, *collaris*, *leucoptera*, *luctuosa*, *bouvreuil* and *hypoxantha* present the highest incidence of sympatry in the genus. Such a situation is seemingly the result of their extensive, often nearly continental, distributions. Equally important is the fact that these distributions, or parts thereof, fall in the sector where the greatest species concentration has been recorded, between 10°S and 20°S (Fig. 2). Although these preliminary results are as accurate as possible at this time, they are likely to be modified significantly when new data become available.

Zoogeographic 'rules'

There appear to be no obvious examples of Bergmann's or Gloger's ecogeographic rules among the polytypic species of the genus *Sporophila*. Graves (1991) has recorded clines in the body size of Andean *Diglossa* and only an equally careful analysis of body size, as well as a careful examination of colouration, will allow a verification of these principles in *Sporophila*, particularly in those species with extensive ranges.

Sick (1991: 40) recently stated: "The Biscutate Swift is one more example from South America of the tendency for populations near the equator to be smaller in size than those at higher latitudes". He cites several examples including one in the Emberizinae, *Oryzoborus angolensis*, to illustrate his findings and adds that "Such geographical variation warrants recognition in the nomenclature" (Sick 1991). Sick's Rule, as this phenomenon may be designated, has yet to be demonstrated in the polytypic species of the genus *Sporophila*, although there are vague indications that populations of some of its species may have slightly smaller body dimensions near the equator; but the adaptive or evolutionary implications of this hypothesis need yet to be demonstrated and explained.

Taxonomic problems

Taxonomic questions associated with the genus *Sporophila* are numerous and complex and take place at 3 levels: higher categories, genus and species. Recent proposals support inspiring theories but have provided few answers to long standing problems.

Higher categories

The history of the higher categories to which the genus *Sporophila* has been associated has been summarized in Sibley & Ahlquist (1990). Based on evidence resulting from DNA-DNA hybridization studies, they conclude that seedeaters are closely related to typical tanagers (Bledsoe 1984, Sibley & Alquist 1990: 683). The genus *Sporophila* has thus been classified in the Tribe Thraupini, Subfamily Emberizinae, Family Fringillidae (Sibley & Alquist 1990, Sibley & Monroe 1990). This classification diverges significantly from more traditional ones where the genus *Sporophila* is placed in the Family Emberizidae and Subfamily Emberizinae (Paynter & Storer 1970, Morony *et al.* 1975, American Ornithologists' Union 1983), and it requires corroboration based on the analysis of a wider selection of taxa, particularly those that were not included in the DNA comparisons, before it can be adopted universally.

The genus

Ridgway (1901) gave a detailed summary of the characteristics of the genus *Sporophila* and pondered over the great differences found between several species included in it. A genus like *Sporophila*, which incorporates a large number of morphologically different species, is not likely to generate unanimity among taxonomists unless solid criteria are selected for defining its limits. Morphological characters presently need to be reassessed and compared with the biochemical and genetic information that will ensue from future studies before a more stable systematic basis can be established for this genus and the other closely related genera. In the interim, the relationships between *Sporophila* and other genera remain uncertain; for example, the genera *Dolospingus*, *Oryzoborus*, *Tiaris*, *Volatinia* and *Loxigilla* are among those which, in addition to sharing many morphological characters found in *Sporophila*, may prove to be even more closely related than is suspected.

The species

A large proportion of the species of the genus *Sporophila* are generally accepted and are, for the most part, well defined, but the situation is more ambiguous for a few of them (Table 1) and several categories of taxonomic problems can be identified at the species level. Four currently recognized species may eventually be treated as hybrids whose origin is practically unknown: *ardesiaca* (Sick 1962, 1963), *melanops*, *insulata* and *zelichi* (Vuilleumier & Mayr 1987, Ridgely & Tudor 1989). Other species may eventually be treated as subspecies of other clearly identified taxa like *bouvronides* [*lineola*], *ardesiaca* [*nigricollis*], *insulata* [*telasco* or *minima*] and *hypoxantha* [*minuta*]. Oppositely, the nominate *S. leucoptera* (including *S. l. cinereola*) and *S. l. bicolor* may be 2 separate species, as indicated by Ridgely & Tudor (1989) rather than 2 subspecies. Similar situations prevail in other species such as *S. intermedia* and *lineola* and require additional study. Yet a few others may be nothing more than colour morphs or aberrant individuals of other taxa: *ardesiaca* [*nigricollis*], *melanops* [*nigricollis*] (Ridgely & Tudor 1989), *hypochroma* [*cinnamomea*], *palustris* [*hypoxantha*], *ruficollis* [*hypoxantha*] (Short 1969, 1975) and *zelichi* [*cinnamomea*]; while some have been treated recently as allospecies of superspecies: *bouvronides* [*lineola*], *hypoxantha* [*minuta*] and *hypochroma* [*cinnamomea*] (Sibley & Monroe 1990). Thus, the variety of taxonomic opinions and treatments given to the taxa of this genus, makes it essential to acquire additional morphological, ecological and behavioural information, as well as biochemical and genetic data, to determine their status and affinities.

Subspecies

Much work remains also to be done at the subspecies level. Geographic variation has been thoroughly studied in only a few species like *S. americana* (Olson 1981b) and the definition, status and distribution of many others is incompletely known. The polytypic species, particularly those with widely disjunct populations like *S. plumbea*, and those with a wide distribution, need to be reviewed and geographic variation assessed in the light of new material and techniques.

References:

American Ornithologists' Union. 1983. *Check-list of North American Birds*. Sixth Edition. Washington, D.C.: American Ornithologists' Union., pp. i–xxix, 1–877.

Bledsoe, A. H. 1984. The phylogeny and evolution of the New World nine-primaried Oscines as indicated by DNA-DNA hybridization. Yale University, Doctoral Dissertation: i–viii, 1–155.

Clark, G. A. 1986. Systematic interpretation of foot-scute patterns in Neotropical finches. *Wilson Bull.* 98(4): 594–597.

Collins, C. T., & Kemp, M. H. 1976. Natal pterylosis of *Sporophila* finches. *Wilson Bull.* 88(1): 154–157.

Graves, G. R. 1991. Bergmann's rule near the equator: latitudinal clines in body size of an Andean passerine bird. *Proc. Natl. Acad. Sci. U.S.A.* 88: 2322–2325.

Haffer, J. 1985. *Avian Zoogeography of the Neotropical Lowlands*. Ornith. Monog. 36: 113–146.

Haffer, J. 1987. Biogeography of Neotropical Birds. *In*: T. C. Whitmore and G. T. Prance (eds): *Biogeography and Quaternary History in Tropical America*. Oxford: Clarendon Press, pp. 105–150.

Hellmayr, C. E. 1938. Catalogue of birds of the Americas and the adjacent islands in Field Museum of Natural History. *Field Mus. Nat. Hist. Zool. Ser.* 13 (11): 1–662.

Lordello, L. G. E. 1957. Duas aves híbridas da fauna do Brasil. *Rev. Brasil. Biol.* 17(1): 139–142.

Meyer de Schauensee, R. M. 1952. A review of the genus *Sporophila*. *Proc. Acad. Nat. Sci. Philadelphia* 54: 153–196.

Monroe, B. L., Jr. 1968. *A Distributional Survey of the Birds of Honduras*. Ornithological Monographs No. 7: 1–458.

Morony, J. J., Jr., Bock, W. J. & Farrand, J., Jr. 1975. *Reference List of the Birds of the World*. New York: American Museum of Natural History, pp. i–x, 1–207.

Narosky, S. 1977. Una nueva especie del género *Sporophila* (Emberizidae). *El Hornero* 11(5): 345–348.

Olson, S. L. 1981a. A revision of the subspecies of *Sporophila* ('*Oryzoborus*') *angolensis* (Aves: Emberizinae). *Proc. Biol. Soc. Washington* 94(1): 43–51.

— 1981b. The nature of the variability in the Variable Seedeater in Panama (*Sporophila americana*: Emberizinae). *Proc. Biol. Soc. Washington* 94: 380–390.

Paynter, R. A., Jr. & Storer, R. W. 1970. *Check-list of Birds of the World*. Volume 13. Cambridge: Museum of Comparative Zoology, pp. i–xiv; 1–443.

Ridgely, R. S. & Tudor, G. 1989. *The Birds of South America*. Volume 1. *The Oscine Passerines*. Austin, Texas: University of Texas Press, pp. 1–xvi, 1–516.

Ridgway, R. 1901. *The Birds of North and Middle America. Part 1*. Bull. U.S. Nat. Mus. 50: i–xvii, 1–715; plates.

Schwartz, P. 1975. Solved and unsolved problems in the *Sporophila lineola/bouvronides* complex (Aves: Emberizidae). *Ann. Carnegie Mus.* 45(14): 277–285.

Short, L. L., Jr. 1969. Relationships among some South American seedeaters (*Sporophila*), with a record of *S. hypochroma* for Argentina. *Wilson Bull.* 81(2): 216–219.

— 1975. A zoogeographic analysis of the South American Chaco avifauna. *Bul. Amer. Mus. Nat. Hist.* 154(3): 163–352.

Sibley, C. G. & Ahlquist, J. E. 1990. *Phylogeny and Classification of Birds: a study in Molecular Evolution*. New Haven, Connecticut: Yale University Press, pp. i–xxiii, 1–976.

Sibley, C. G. & Monroe, B. L., Jr. 1990. *Distribution and Taxonomy of Birds of the World*. New Haven, Connecticut: Yale University Press, pp. i–xxiv, 1–1111.

Sick, H. 1962. Reivindicaçao do papa-capim *Sporophila ardesiaca* (Dubois). Sua ocorrência no Brasil (Fringillidae-Aves). *Bol. Mus. Nac. Nov. Sér. Rio de Janeiro—Brazil* 235: 1–23.

— 1963. Hybridization in certain Brazilian Fringillidae (*Sporophila* and *Oryzoborus*). *Proc. XII Internat. Ornithol. Congr. 1962* 1: 161–170.

— 1991. Distribution and subspeciation of the Biscutate Swift *Streptoprocne biscutata*. *Bull. Brit. Orn. Cl.* 111(1): 38–40.

Vuilleumier, F. & Mayr, E. 1987. New species of birds described from 1976 to 1980. *J. Ornithol* 128(2): 137–150.

Wolters, H. E. 1980. *Die Vogelarten der Erde*. Volume 5. Berlin: Paul Parey, pp. 321–400.

Address: Dr. Henri Ouellet, Canadian Museum of Nature, P.O. Box 3443, Station «D», Ottawa, Canada. KIP 6P4.

© British Ornithologists' Club 1992

Emergence of hybridogenous polymorphism in the *Oenanthe picata* complex

by E. N. Panov

Received 14 May 1992

The simultaneous existence in a population of 2 or more discrete phenotypes ('morphs', 'phases', 'varieties') belonging to one sex and age-class (e.g. sexually mature males) is generally known as genetic polymorphism. Although polymorphism of this kind is by no means rare in birds, many questions concerning the causal relationships and biological significance of the phenomenon remain open. One such question concerns the mechanisms by which polymorphism originates within a population.

Alongside the prevailing view that polymorphism is caused by a process of mutation (i.e. spontaneous events taking place purely within a given population), the idea has also been expressed that it may have evolved on the basis of gene exchange between originally independent populations (see e.g. Haffer 1977: 41).

In this paper an attempt will be made to reconstruct the historical process which led to 'hybridogenous polymorphism' (see Panov 1989), and other types of variation resulting from hybridization, in Palaearctic wheatears of the *Oenanthe picata* complex. Until recently, geographical variation in this complex was generally treated as a variation in the relative numbers of 3 colour 'varieties' or 'morphs' (*picata, capistrata* and *opistholeuca*). The origin of this supposedly discrete variation was seen in terms of changes in the frequency of alleles of certain genes responsible for male plumage coloration (e.g. Mayr & Stresemann 1950, Paludan 1959, Loskot 1972, Stepanyan 1978).

Our hypothesis (Panow 1974, Panov 1989) is based on a completely different premise, namely that the 3 plumage types in the Eastern Pied Wheatear *O. picata* in fact characterize 3 originally independent taxa, each of which evolved in its autochthonous range in accordance with the principles of geographical speciation. The present distribution pattern of individuals with the 3 different plumage types (and also of various 'intermediate' phenotypes) is explained by the processes whereby the gene pools of the 3 original populations became intermixed.

We shall examine here the 3 main types of integration processes which correspond to the varying nature and intensity of gene flow between erstwhile independent population systems.

1. Limited hybridization in places where the breeding ranges of the original forms abut (parapatry) or overlap to an insignificant extent (allo-parapatry). The result may be the formation of a narrow zone of hybridization.

2. Prolonged existence of such a zone may lead to the establishment of gene flow from the zone of hybridization into the ranges of the parent forms. Gene migration takes place through the generations and also through dispersal by individuals of one form into the range of another and by birds of hybrid origin straying into the ranges of both forms.

3. Should hybridization become more firmly established, the hybrid zone may expand and a panmictic hybridogenous population with polymorphic features be created, which will eventually acquire a range of its own.

In the years 1966–1990, we studied the phenotypic composition of Eastern Pied Wheatear populations at 10 localities in the bird's Central Asian breeding range. A total of 279 males and 168 females was trapped, and 347 chicks were individually marked, 34 of these being retrapped in subsequent years. Twenty-eight chicks were reared in captivity until they had acquired adult plumage, and 296 specimens (217 males, 79 females) were examined in museum collections.

Divergence within the 'Eastern Pied Wheatear' complex

Plumage colour and sexual dimorphism

The 3 forms which constitute this complex were originally described as independent species under the names *Saxicola picata* Blyth, 1847, *S. opistholeuca* Strickland, 1849, and *S. capistrata* Gould, 1865. They are well differentiated in plumage coloration, not only of males but also females (Fig. 1) and, perhaps, also in juvenile plumage (Zarudnyi 1923).

Unlike the 2 others, the form *capistrata* shows clear sexual dimorphism, females being distinguished from males by the complete absence of melanins in their plumage. In the forms *picata* and *opistholeuca*, female plumage is variable, and females which are virtually indistinguishable from males are not uncommon (Panov 1989) (Fig. 2). There is some basis for the supposition that the contrasting male-type plumage is acquired by female *picata* and *opistholeuca* with age (Panov *et al.* in press).

Biometrics

In those parts of its range where it is not in contact with the other 2 forms, *picata* has a significantly shorter wing than populations from the autochthonous ranges of *capistrata* and *opistholeuca*. Maximum wing-length tends to be characteristic of populations from northern parts of the autochthonous range of *capistrata*, far from the ranges of the other 2 forms (Table 1; see also Panov *et al.* in press). Wing-length in this case is probably a reliable indicator of general body-size.

The weight of *picata* males from various localities in Turkmenistan ranges from 19.7 ± 0.2 g to 21.5 ± 0.4 g (mean of whole sample of 102 males 20.2 ± 0.2 g). Similar values are quoted by Desfayes & Praz (1978) for southern Iran. Our sample of *picata* males differs significantly ($t = 4.69$, $P < 0{\cdot}001$) from a sample of 6 males from the autochthonous range of *capistrata* (23.3 ± 0.6 g). The latter value matches weight data for 10 *capistrata* males (23.5 ± 0.5 g) from northern Afghanistan (see Paludan 1959). Further data in Paludan (1959) indicate a mean weight of 21.7 ± 0.4 g for 8 *picata* males from western Afghanistan, and 22·1 ± 0·33 g for 10 *opistholeuca* males from the autochthonous range of that form; the differences between *capistrata* and *picata* are significant ($t = 3.1$, $P < 0{\cdot}01$), also those between *capistrata* and *opistholeuca* ($t = 2.4$, $P < 0{\cdot}05$); between *picata* and *opistholeuca* the differences are not significant ($t = 0.77$).

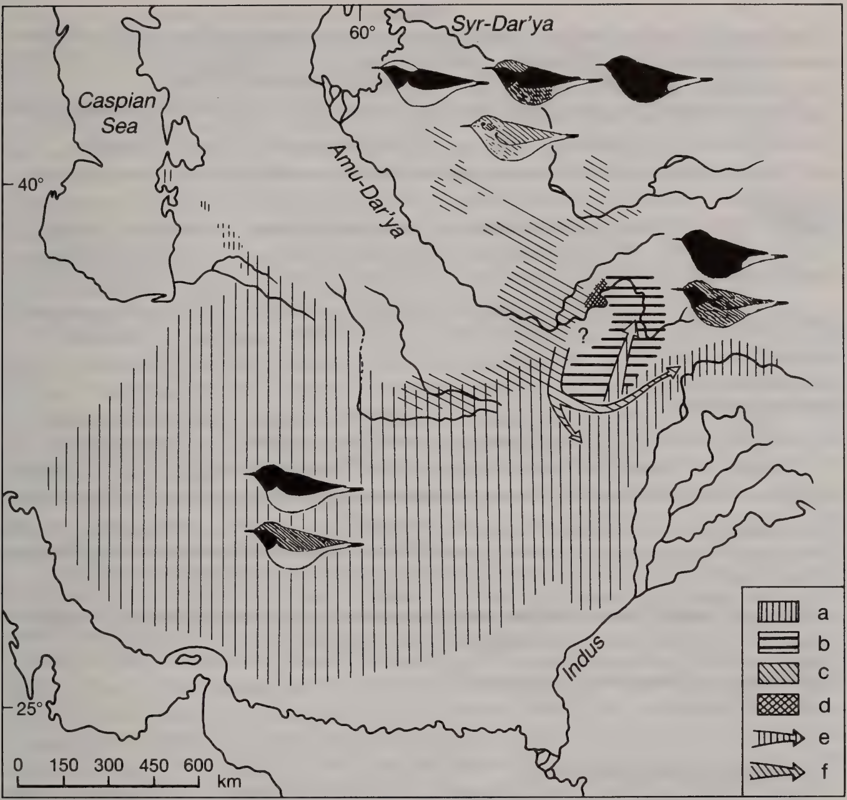


Figure 1. Ranges of the form (a) *picata* (b) *opistholeuca*, (c) polymorphic hybridogenous population '*capistrata* × *opistholeuca*' and (d) hybrid population '*capistrata* × *opistholeuca*' × *opistholeuca*. Main directions of dispersal by the form *picata* into the range of (e) *opistholeuca* and (f) by individuals of the *capistrata* pehnotype into the range of *picata* are indicated by arrows.

Top row:	♂ *capistrata*	♂ *evreinowi* ♀ *evreinowi*	♂ *opistholeuca*
Middle row:			♂ *opistholeuca* ♀ *opistholeuca*
Bottom row:	♂ *picata* ♀ *picata*		

Decreasing body-size in the order *capistrata*—*opistholeuca*—*picata* is also reflected in the different egg dimensions.

Eggs of pairs with *capistrata* males are significantly larger (in width) than eggs from clutches of the form *picata* in its autochthonous range (16.0 ± 0.6, $n = 62$ and 15.5 ± 0.09, $n = 49$, respectively; $t = 4.55$, $P < 0{\cdot}0002$). Eggs of the form *opistholeuca* occupy an intermediate position in this parameter (15.7 ± 0.10 mm, $n = 35$).

TABLE 1

Means (mm) ± standard deviation, sample size and range (mm) of wing-length (unflattened chord) of Eastern Pied Wheatears, the *Oenanthe picata* complex, from autochthonous ranges of the forms *picata, capistrata* and *opistholeuca*

	Males >1 year	1st-year males	Females
Range of:			
picata	90.4 ± 0.2 ($n=110$)	88.0 ± 0.2 ($n=81$)	85.7 ± 0.3 ($n=81$)
	84.0–95.3	84.6–92.3	75.9–89.9
opistholeuca	92.3 ± 0.3 ($n=24$)	90.3 ± 0.5 ($n=10$)	87.1 ± 0.3 ($n=20$)
	88.2–95.3	87.0–92.0	85.1–89.9
*capistrata**	92.9 ± 0.3 ($n=61$)	90.5 ± 0.3 ($n=45$)	87.1 ± 0.3 ($n=38$)**
	88.0–97.7	86.3–94.4	83.0–92.6
Comparison by Student's t-test			
1:2	$t=5.28$, $P=0.0001$	$t=4.22$, $P=0.0002$	$t=3.41$, $P=0.001$
1:3	$t=8.10$, $P=0.00001$	$t=6.51$, $P=0.00004$	$t=2.97$, $P=0.01$
2:3	$t=1.53$, $P=0.14$ (n.s.)	$t=0.28$, $P=0.78$ (n.s.)	$t=0.07$, $P=0.96$ (n.s.)

*Hybridogenous polymorphic populations '*capistrata* × *opistholeuca*'. Analysis of combined sample comprising the phenotypes *capistrata, opistholeuca* and *evreinowi* (differences between samples of these phenotypes within this population group are not significant).

**In this sample 24 females are from the southern part of the range of the populations investigated, where there is perhaps some influence from genes of the small form *picata*. Mean for 14 females from northern part of the range of '*capistrata* × *opistholeuca*' populations is 88.6 ± 0.5 mm (difference from mean of females from autochthonous range of *opistholeuca* significant, $t=2.49$, $P=0.05$).

Communication behaviour

We compared the vocalizations of the 3 forms of Eastern Pied Wheatears, the motor patterns of their communication behaviour and the organization of the main types of social interactions (Kostina & Panov 1981, Panov 1989). As a whole, the communication systems of these forms are structurally identical, though their component elements are subject to considerable variation. Because of this, data presented here on apparent quantitative differences between some homologous components are best regarded as provisional.

Of the 6 call- and 4 song-types characteristic of all 3 forms, differences were found in one call-type—in *picata* and *capistrata* (data for *opistholeuca* are insufficient for comparison)—and 2 song-types. Advertising song differs most conspicuously from the general type in the form *opistholeuca* in its autochthonous range.

The motor patterns of communication behaviour appear identical, apart from certain tendencies for variation in the frequency with which particular elements of the patterns are used by one or another of the 3 forms. Comparison of the organization of behaviour during pair-formation found *capistrata* females to be more aggressive than *picata* females. Pre-copulatory interactions are very similar in the forms *picata* and *opistholeuca*, but they differ from those of *capistrata*, whose behaviour in this context is closer to Finsch's Wheatear *O. finschii*.

Habitat and timing of breeding season

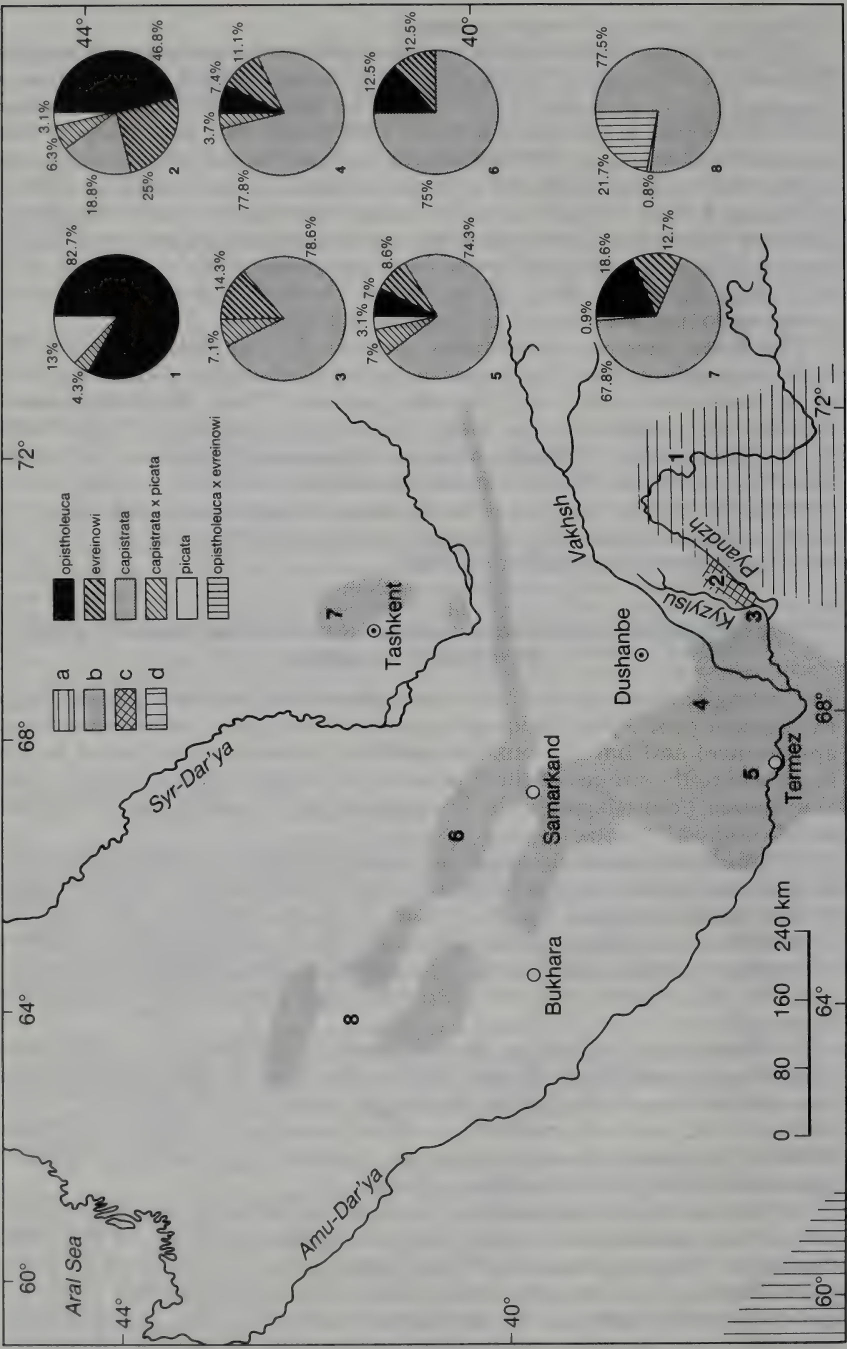
The form *capistrata* inhabits arid low hills and clearly avoids nearby high-mountain massifs. In the area of the former USSR, it ascends as a breeding bird to altitudes of c. 1500 m. The form *opistholeuca* is found up to 2000–2500 m in the Pamiro-Alay, with *picata* also ascending to that altitude from the south. In the mountains of southern Iran, *picata* breeds in the zone between 2100 and 2400 m, occasionally ascending to 2700 m (Desfayes & Praz 1978). Originally typical inhabitants of rocky mountain habitats, *picata* and *opistholeuca* are spreading into broken semi-desert terrain originally occupied by the form *capistrata*, with which they now hybridize. In these areas of secondary contact, individuals of all 3 phenotypes nest side by side in the same habitats.

The form *capistrata* is probably prevented from expanding into the high-mountain parts of the ranges occupied by the other 2 forms because of its characteristically early breeding season. Thus, the start of nest-building by *capistrata* has been recorded in southern Uzbekistan (c. 38°N) around 6–15 March, while at approximately the same latitude in Badkhyz (southeast Turkmenistan) *picata* does not begin nesting before 5–12 April. During this period in the range of *opistholeuca*, near where it abuts *capistrata*, arrival of females and pair-formation are not yet concluded (for details see Panov 1989).

Hybridization and its consequences within the 'Eastern Pied Wheatear' complex

According to the proposed hypothesis, there exist within the complex at the present time 3 population groups with a relatively stable phenotypic appearance, and populations intermediate between them found in the areas where the ranges of the 3 population groups referred to above are contiguous, or overlap or both. The phenotypically stable populations are as follows:

1. Populations generally with the diagnostic features of the form *picata* (which has the largest area of distribution in western and southern parts of the range occupied by the whole *O. picata* complex: see Fig. 1). Throughout the range, birds with some white on the head (tendency towards *capistrata* phenotype) are common alongside typical males. Locally, the proportion of such 'aberrant' males reaches 70% (see below for details);
2. Populations showing the diagnostic features of *opistholeuca* (Badakhshan and Hindu Kush). Within the range of these populations a few individuals of the *picata* phenotype occur (not more than 10%). While mixed pairs are evidently a quite common phenomenon (Panov 1989: 87), males showing plumage features intermediate between *opistholeuca* and *picata* are extremely rare;
3. Polymorphic hybridogenous populations '*capistrata* × *opistholeuca*', which presumably now occupy the autochthonous range of the form *capistrata*. They are found in the northeast part of the range of the complex (Figs. 1, 3). Over the whole range of these populations, there is a generally stable ratio of the phenotypes *capistrata* (the overwhelming majority), *opistholeuca*, and birds of the extremely variable phenotype


a
b
c
d
opistholeuca
evreinowi
capistrata
capistrata x picata
picata
opistholeuca x evreinowi
1
82.7%
13%
4.3%
2
46.8%
3.1%
6.3%
18.8%
25%
3
78.6%
14.3%
7.1%
4
11.1%
7.4%
3.7%
77.8%
5
74.3%
8.6%
7%
3.1%
7%
6
12.5%
12.5%
75%
7
12.7%
18.6%
0.9%
67.8%
8
77.5%
21.7%
0.8%
44°
40°
60°
64°
68°
72°
Aral Sea
Syr-Dar'ya
Amu-Dar'ya
Tashkent
Samarkand
Bukhara
Dushanbe
Termez
Vakhsh
Pyandzh
Kyzylsu
0
80
160
240 km

evreinowi, intermediate between these 2. In the south of the range, in sections contiguous with *picata*, are found small numbers of *picata* males and *picata* × *capistrata* hybrids (total 5.6–11.4%).

In the contact zones of the last group of populations with the 2 others, live hybrid populations whose phenotypic composition is highly variable in space and probably also in time occur. Such populations are known from northeast Afghanistan (Paludan 1959), and from the interfluve of the Pyandzh and Kyzylsu in Tadzhikistan. In addition, a hybrid population may perhaps exist where the ranges of *opistholeuca* and *picata* meet in northeast Pakistan, and where the form *capistrata* also penetrates via large river valleys from the northwest (Ticehurst 1922, Paludan 1959; see Fig. 1).

Below, we shall examine in more detail: (1) the situation in the range of the polymorphic hybridogenous population *capistrata* × *opistholeuca*; (2) the zone of hybridization found where the range of that population meets the autochthonous *opistholeuca* populations in Tadzhikistan; and (3) the introgression of *capistrata* genes from the polymorphic *capistrata* × *opistholeuca* population into the autochthonous range of *picata* in southern Turkmenistan.

1. *Polymorphic hybridogenous populations* 'capistrata × opistholeuca'

These populations inhabit low hills in the east of Central Asia and northern Afghanistan—from the relict mountains ('Inselberge') of the Kyzylkum desert in the north to the northern foothills of the Paropamiz and Hindu Kush in the south. Throughout their range (which measures c. 750 m west to east by c. 200 km north to south), they are relatively monotypic in phenotypic composition: among males, the *capistrata* phenotype makes up 68–78% of different samples, and the *opistholeuca* phenotype and *evreinowi*—to all intents and purposes united in a single continuum of variability—from 17.5 to 32%. (The *picata* and *picata* × *capistrata* phenotypes are normally present only in the southernmost parts of the range of these populations—see above and Fig. 3.)

It is quite remarkable that the polymorphism of male plumage coloration is combined with the monomorphic plumage of females: practically all females show the same dull sand-coloured plumage type. Dark (brown-black) females of the *opistholeuca* type are virtually absent from the range of these populations.

Data from the individual marking of birds in the northern range of these groups of populations (Darbaza settlement in southern Kazakhstan, north of Tashkent) indicate the absence of strict mate-selection on

Figure 3. Proportions of different phenotypes (%%) in the autochthonous range of (a) *opistholeuca*, (b), in the range of a polymorphic population '*capistrata* × *opistholeuca*' and (c) in a hybrid population '*capistrata* × *opistholeuca* × *opistholeuca*' and (d) the range of the form *picata*. Male phenotypes: (e) *opistholeuca*, (f) *evreinowi*, (g) *capistrata*, (h) *capistrata* × *picata*, (i) *picata*. Places where the samples were obtained: 1 = Tadzhik Badakhshan (25 males), 2 = Pyandzh-Kyzylsu interfluve (62), 3 = Karatau mountains (14), 4 = Babatag mountains (27), 5 = lower reaches of Sherabad river (128), 6 = Nuratau mountains (16), 7 = western foothills of Karzhantau mountains (192), 8 = relict mountains in Kyzylkum desert (Aktau, Tamdytau, Bukantau) (129).

plumage type. As may be seen from the table below, a female having a father of her own phenotype (e.g. *capistrata*) may select as a mate a male of a different phenotype:

Phenotypes of females' fathers	Phenotypes of females' mates *capistrata*	*opistholeuca*	Total number of pairs
capistrata	8	2	10
opistholeuca	3	2	5
Total number of pairs	11	4	15

Individual marking also showed that one and the same female may breed with males of different phenotypes in different years.

Support for the hypothesis of genetic polymorphism comes from the inherited plumage characteristics of sons sired by fathers of known phenotypes. As follows from the table below, the progeny of a male of given phenotype may include males of a different phenotype:

Phenotype of fathers	Phenotype of sons *capistrata*	*opistholeuca*	*evreinowi*	Total number of sons
capistrata(12)	14	—	1	15
opistholeuca(4)	2	2	2	6
evreinowi(4)	6	3	2	11
Total number of sons	22	5	5	32

Two of the 4 male *evreinowi* fathers had a plumage type intermediate between *capistrata* and *opistholeuca*; the 2 others were of the *opistholeuca* colour type, with only a slight tendency towards *capistrata*.

It is interesting that males of different phenotypes may be present even within the same brood. In 2 cases we were able to trace the inherited colour pattern through more than one generation. In one such line, the son, his father and grandfather were of the same *opistholeuca* phenotype. In another case, a *capistrata* male having father and grandfather of the same phenotype paired and bred with a female whose father was an *opistholeuca* male. The progeny of this pair included 2 males, one of which was of the *capistrata* phenotype, the other *evreinowi*.

The aforesaid allows the conclusion that the populations considered here represent a genetically homogeneous entity which we suppose to have arisen as a result of penetration by the form *opistholeuca* into the range of *capistrata* and long-term hybridization between them. It may well be that the form *capistrata* no longer exists at the present time as an independent genetic system.

2. *Hybrid population found where the polymorphic population* 'capistrata × ophistholeuca' *abuts the range of the autochthonous form* opistholeuca

In the southeast of western Tadzhikistan, in the interfluve of the Pyandzh and its tributary the Kyzylsu, studies were made on a transect (of c. 100 km) running from southwest to northeast between the foothills of the Karatau range on the east bank of the Kyzylsu and the eastern slopes of the Khazretishi mountains (Khirmandzhou settlement—see Lyubushchenko & Grabovskiy 1991, and Panov *et al.* in press). Between the Karatau and Khazretishi ranges lies the South Tadzhik depression with its single, completely isolated mountain Khodzhamumin.

The population of the Karatau foothills is part of the polymorphic population described above: out of 14 males observed, 11 were of the *capistrata* and 3 of the *evreinowi* phenotype. At the opposite, northeast end of the transect (Khirmandzhou), all 18 males recorded were of the *opistholeuca* phenotype. This population occupies the extreme northwest section of the autochthonous *opistholeuca* range.

In the area lying between the points named, on the southern and eastern edge of the South Tadzhik depression and on the slopes of Mt Khodzhamumin, a further 5 demes of 6–24 pairs were studied. The phenotypic composition of such demes is highly variable. Overall, the ratio of *capistrata, opistholeuca* and *evreinowi* phenotypes in these 5 demes was 25.8: 48.4: 24.8 ($n=62$), which is significantly different from the composition of all populations from the range of the polymorphic entity '*capistrata* × *opistholeuca*' discussed above (ANOVA; $F=7.22$–9.12, $P<0{\cdot}00001$).

It is important also that here, unlike in the polymorphic population referred to, female plumage colour varies: alongside the predominant *capistrata* type, *opistholeuca*-type females also occur. We thus have before us a heterogeneous (in the genetic sense) hybrid population in which there has been no stabilization of a monomorphic female phenotype such as is taking place in the hybridogenous polymorphic population '*capistrata* × *opistholeuca*'.

Among the 96 males observed on the transect, 2 were *picata* phenotypes and 3 had plumage intermediate between *picata* and *capistrata*. Two out of 43 females were also of the *picata* plumage type. This small admixture of the *picata* phenotype (5.2% among males) is presumed to be the result of dispersal by individuals of this form from northern parts of the *picata* range lying not far to the south.

3. Migration of capistrata *genes into the autochthonous range of the form* picata

We assessed the proportion of *picata*-type males with some white on the head at 4 points on a transect leading along the northwest edge of the *picata* range in southern Turkmenistan. The easternmost point on this transect lies approximately 200–300 km from the contact zone of *picata* and '*capistrata* × *opistholeuca*' populations in north-central Afghanistan (see Paludan 1959). The 3 other samples were collected at points separated from the first and one from another by distances of the same order (Fig. 4). The amount of white in male head plumage was scored on an 8-point scale: 0—pure *picata* phenotype, 7—phenotypically pure *capistrata*.

It is clear from Fig. 4 that males with some white on the head are not uncommon throughout that part of the *picata* range investigated, and in some areas they even outnumber males of the pure phenotype. The cause of this plumage feature in *picata* populations may be: (1) the existence of homologous genes in populations of *picata* and *capistrata*; and (2) introgression of *capistrata* genes into the range of *picata*. In the latter case, the migration of genes may (a) proceed through the generations (owing to

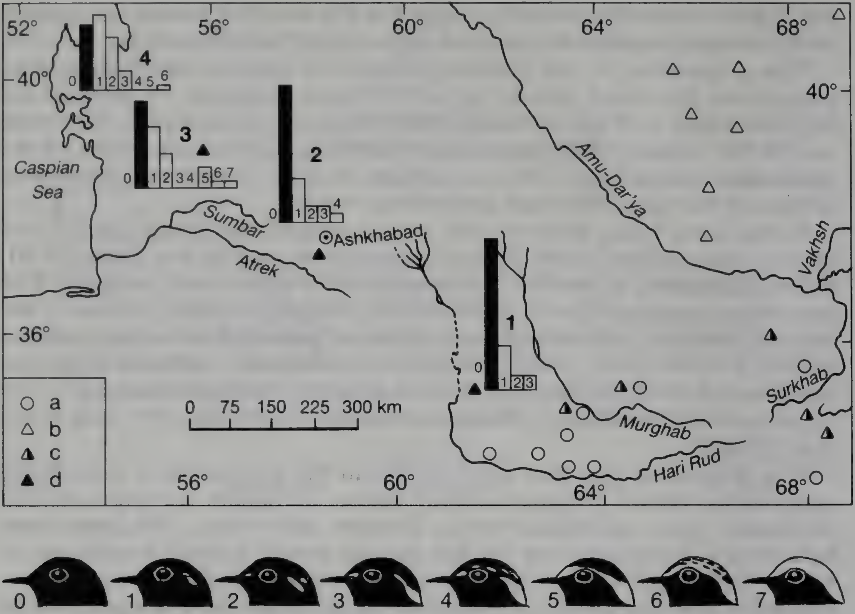


Figure 4. Proportion of males with different head colour (%%). Point 1 = Badkhyz ($n = 16$); Point 2 = central Kopet-Dag ($n = 38$); Point 3 = western Kopet-Dag ($n = 33$); and Point 4 = near Krasnovodsk ($n = 57$). Head colour scored on point-scale: 0 = pure *picata*; 7 = pure *capistrata*, 1–6 = intermediate ('hybrid') phenotypes. a = records of *picata* on its northern range limit in Afghanistan (from Paludan 1959); b = westernmost records of *capistrata* phenotype males in the USSR; c = records of *capistrata* in northern Afghanistan (Paludan 1959); d = records of breeding *capistrata* in the range of *picata*. In the histograms, the extreme left column (black) shows the proportion in the given sample of typical black-headed *picata* males (score 0). The white columns right of the black column are shown in order of increasing point score (1, 2, 3, and so on).

back-crossing of hybrids, originating in the secondary contact zone of the 2 forms, with representatives of *picata* populations from its autochthonous range), and (b) may result from dispersal by individuals of the form *capistrata* into the range of *picata*.

None of these possibilities can be refuted, but we are inclined to support the hypothesis of gene introgression and, as evidence in favour of supposition 2b, we can at least cite the case of a *capistrata* male paired and breeding successfully with a *picata* female in the central Kopet-Dag (point 3 in Fig. 4; see also Bel'skaya 1961). Furthermore, supposition 2a appears to be contradicted at first sight by an increase in the proportion of 'white-headed' males with increasing distance from the range of *capistrata*.

The latter circumstance may nevertheless be reconciled with the hypothesis of gene migration if one rejects the idea that the flow of alien genes across the range of *picata* is uniform in space and in time. In particular, the dynamics of phenotypic composition may, in principle, be influenced not only by the distance separating a given population from the source of an alien gene pool, but also by the extent of its separation from other birds of genetically the same stock. In this regard, it is significant that the plumage feature of partial 'white-headedness' has its widest distribution in the western Kopet-Dag and in the low hills of the south-east Caspian region, where suitable *picata* nesting habitat is patchily distributed rather than uniformly as in the central Kopet-Dag. In semi-isolated demes inhabiting widely separated mountain ranges, new plumage features can become fixed comparatively quickly, such features in the present case having been introduced into the given deme by alien *capistrata* genes (for further details, see Panov *et al.* in press).

Discussion

According to the proposed scenario, the 'Eastern Pied Wheatear' complex is a standard polytypic species comprising 3 geographical races, all of which were originally monomorphic in respect of male plumage colour. These races separated off and diverged in conditions of geographical isolation and then, as a result of range expansion, entered into secondary contact and hybridization.

It was precisely the mixing of the gene pools of the 3 originally autonomous population groups which determined that phenotypic dissimilarity in Eastern Pied Wheatears which is generally called 'polymorphism'. In our view, this concept is, in its generally accepted sense (see e.g. Mayr & Stresemann 1950), not applicable to the case under investigation. In fact, what we have before us is either 'pseudo-polymorphism' (see Panov 1989), i.e. the simultaneous existence of representatives of 2 or 3 *different taxa* in the area of their secondary contact (as is the case, for example, in the Pyandzh-Kyzylsu interfluve), or 'hybridogenous polymorphism' which has arisen as a result of long-term introgressive hybridization (of the population '*capistrata* × *opistholeuca*').

Taking this scenario as a whole, it may be assumed that the first stage in its development was the simultaneous separation of a single ancestral species into 3 population groups. One of these (the present-day *picata*) separated off in the Iranian highlands; the second (*opistholeuca*) in the western mountain regions of Central Asia; the third (*capistrata*) originally inhabited the lower parts of the western Gissaro-Alay mountains and adjoining areas.

The latter scheme cannot completely accommodate a number of facts which (if they have been correctly interpreted) may indicate that the forms in question have attained different levels of divergence and, therefore, may differ one from another genealogically (i.e. in evolutionary age). One gains the impression that *picata* and *opistholeuca* are most probably sister taxa, while *capistrata* stands somewhat apart. This supposition gains strength from the fact that *picata* and *opistholeuca* on the one hand and *capistrata* on the other differ with respect to the type of sexual dimorphism, particular features of communication behaviour, and preferred habitats.

After consideration of the foregoing, one may imagine 2 ways in which the *Oenanthe picata* complex may have emerged. The first option envisages a single ancestral form originally splitting into 2 population groups which may provisionally be called 'low-mountain' and 'high-mountain'. The first group eventually produced the form *capistrata*, the second split in the course of time into the forms *picata* and *opistholeuca*.

The second option supposes the complex to have emerged through 2 successive invasions into its present range from the range of ancestral taxa generally believed to be African, Middle Eastern and southwest Asian wheatears of the superspecies *lugens—lugentoides—lugubris* (see e.g. Panov 1989, Tye 1989). Moreover, the immigrants in one case may have come from the range of *lugens*, males of which have the same type of plumage pattern as *capistrata* males and comparatively large measurements. Another wave of colonists may have originated from the range of the *lugubris* group, males of which characteristically have a high degree of pigmentation, which is also a typical feature of the forms *picata* and *opistholeuca* (Tye 1989: 173).

In order to discover which of the proposed scenarios is closest to the truth, there is a need for further comparative investigations within the 'Eastern Pied Wheatear' complex, and also for a comparison of the various representatives of this group with the still little-known wheatears of the *lugens—lugentoides—lugubris* complex. It is recommended that priority in such future studies be given to approaches which focus on comparative ethology and molecular genetics.

Acknowledgements

I am very grateful to Michael G. Wilson, who kindly translated the manuscript into English and Euan Dunn, who made valuable comments, both working at the Edward Grey Institute, Oxford.

References:

Bel'skaya, G. S. 1961. On the ecology of the Eastern Pied Wheatear. *Trudy Inst. Zool. Parasitol. Akad. Nauk Turkmen. SSR* 7: 43–54 (in Russian).

Desfayes, M. & Praz, J. C. 1978. Notes on habitat and distribution of montane birds in southern Iran. *Bonn Zool. Beitr.* 29: 18–37.

Haffer J. 1977. Secondary zones of birds in northern Iran. *Bonn. Zool. Monogr.* 10.

Kostina, G. N. & Panov, E. N. 1981. Individual and geographical variation in the song of the Eastern Pied Wheatear *Oenanthe picata*. *Zool. Zh.* 60: 1374–85 (in Russian).

Loskot, V. M. 1972. Intraspecific variation and systematics of the Eastern Pied Wheatear *Oenanthe picata* (Blyth). *Vestnik Zool.* (4): 28–34 (in Russian).

Lyubushchenko, S. Yu. & Grabovskiy, V. I. (in press). Phenotypic composition of Eastern Pied Wheatear (*Oenanthe picata capistrata* and *O. p. opistholeuca*) in their contact zone in southern Tadzhikistan (in Russian).

Mayr, E. & Stresemann, E. 1950. Polymorphism in the chat genus *Oenanthe*. *Evolution* 4: 291–300.

Paludan, K. 1959. On the birds of Afghanistan. *Vidensk. Medd. Dansk Naturh. Foren.* 122.

Panov, E. N. 1989. *Hybridization and Ethological Isolation in Birds*. Moscow (in Russian).

Panov, E. N., Grabovskiy, V. I. & Lyubushchenko, S. Yu. (in press). Divergence and hybridogenous polymorphism in the 'Eastern Pied Wheatear' complex. *Zool. Zh.* (in Russian).

Panow, E. N. 1974. *Die Steinschmätzer der nördlichen Paläarktis*. Wittenberg Lutherstadt.

Panow, E. N. 1980. Divergenz und Hybridisation in der Gruppe der Elstersteinschmätzer (*Oenanthe picata*). *Mitt. Zool. Mus. Berlin.* 56 *Suppl. Ann. Orn.* 4: 3–23.

Stepanyan, L. S. 1978. *Species Composition and Distribution of Birds in the USSR Fauna. Passeriformes*. Moscow (in Russian).

Ticehurst, C. B. 1922. Notes on some Indian Wheatears. *Ibis* (11)4: 151–8.

Tye, A. 1989. Superspecies in the genus *Oenanthe* (Aves, Turdidae). *Bonn. Zool. Beitr.* 40: 165–82.

Zarudnyi, N. A. 1923. On some chats (*Saxicola picata* Blyth, *S. capistrata* Gould, *S. opistholeuca* Strickl, and *S. opistholeuca evreinowi* Zar.). *Izv. Turkestan. Otd. Russk. Geogr. Obshch.* (Tashkent) 16: 72–81 (in Russian).

Address: Dr E. N. Panov, A. N. Severtsov Institute of Evolutionary Animal Morphology and Ecology, Russian Academy of Sciences, Lenin Avenue 33, Moscow 117071, Russia.

© British Ornithologists' Club 1992

Systematic position and taxonomic level of grouse in the order Galliformes

by R. L. Potapov

Received 26 May 1992

The clear division of the Galliformes (gallinaceous birds) into two groups—the ancient Cracoidea (Cracids and Megapodes) and the younger Phasianoidea—was established when the very first morphological revisions were made and, with rare exceptions (Clark 1960, 1964), has remained undisputed to the present day. The taxonomic status of these 2 groups varies from superfamily to suborder in the classifications proposed by different authors. Dividing the first group (Cracoidea) into the families Cracidae and Megapodiidae was an obvious course, as these differ morphologically and have long been widely separated geographically. The second group (Phasianoidea) differs clearly from the first (Cracoidea) in the position of the hallux on the tarsus, but its taxonomic subdivision is generally rather complex and much less straightforward. Up to the present day, various authors have argued with varying degrees of conviction for the inclusion in the Phasianoidea of the following groups: turkeys, guineafowl, peafowl, pheasants, Old World quails, New World quails and grouse. During the last 2 centuries, all possible combinations seem to have been tried in order to classify these groups, which have been variously given the rank of subfamilies within the single family Phasianidae, treated as separate families, or some united within the Phasianidae, others treated as independent families. However, the most usual classification has been that which treated as separate families the Phasianidae (comprising the subfamilies Odontophorinae, Perdicinae, Phasianinae, Numidinae), Meleagridae and Tetraonidae. New evidence has, however, now been produced which suggests that the guineafowl should be elevated to family rank (Sibley & Ahlquist 1990, Sych 1990).

The diversity of opinion with respect to classification of the Phasianoidea points above all to the low degree of divergence within the superfamily. It may further reflect the universal nature of phasianid morphology, which permits adaptation to a variety of environmental conditions. For example, the New World quails, despite having been separated longest from the main branch of phasianids (Sibley & Ahlquist 1990), have developed so few distinctions from the latter that they have been almost invariably treated by morphologists as only a subfamily within the Phasianidae. This case indicates that the quite considerable differences in DNA between the New World quails and other phasianids (more so than between guineafowl and other phasianids) are barely reflected in their morphology.

We have at least 2 methods for calculating the time of isolation of New World quails. One involves the use of starch gel electrophoresis with the fossil representatives of this group from the mid-Miocene in order to calibrate genetic distances (Gutiérrez *et al.* 1983). Another method focuses on geological and palaeogeographical data from roughly the time

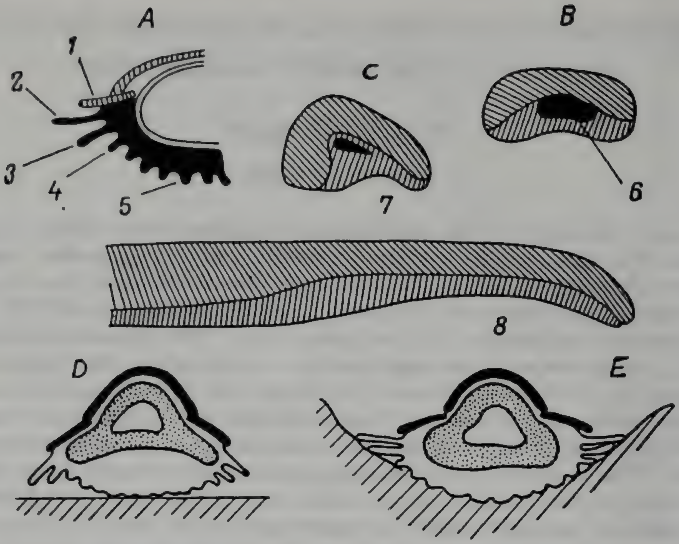


Figure 1. **Horny appendages on toes of grouse.** **A** = cross-section through terminal phalange of Capercaillie (*Tetrao urogallus*). 1 = lateral scutes; 2 = first row of appendages; 3 = second row of appendages; 4 = intermediate protuberance; 5 = foot papillae. **B** = transverse cross-section of growing appendage at its base; 6 = pulp. **C**: 7 = transverse cross-section of horny appendage; 8 = longitudinal cross-section of horny appendages. **D** = position of appendages when toe is in contact with branch. **E** = position of appendages when toe is in contact with snow. (From Potapov 1985.)

of the disjunction of North America and Europe. Interestingly, both methods give the same result: isolation in the lower Oligocene, c. 35 million years ago.

Based solely on DNA-hybridization data, Sibley & Ahlquist (1990) gave the New World quails the rank of family, the grouse that of subfamily. On the contrary, the grouse (which, like the turkeys, undoubtedly diverged much more recently than the New World quails—Sibley & Ahlquist 1990) show distinct morphological, ecological, ethological and, probably, also physiological differences, and we need to discuss the main features of this group separately.

Morphological characteristics of grouse

Pectinated toes

First we should consider a feature which is common to all grouse (with one exception) and not found in any other birds. This is the horny appendages (pectination) along the sides of the toes (Fig. 1). These appendages are shaped like miniature elongated scoops or nails with blunt tips. Forming a single or double row on both sides of the toes, they break and fall off in spring and regrow each autumn before the onset of winter. Only in the willow grouse and ptarmigan (genus *Lagopus*) which live in the most severe climatic conditions are these appendages replaced by thick feathering; the pectination is found, nevertheless, in rudimentary form in one member of the genus *Lapogus*, the White-tailed Ptarmigan *L. leucurus* (in addition it has many relict features), thus giving a clear indication that the feathering of the toes is a secondary development, evolving in place of the appendages. The functional significance of the appendages, which appear only for the winter, is obvious: they more than double the surface area of the foot, which is an important aid not so much to locomotion on such a friable surface as snow (in most cases such walking on the snow is not necessary) as to the need to burrow into the snow 1–3 times per day to escape the severe winter cold. Each horny appendage acts as a miniature scoop, thereby significantly increasing the digging function of the foot and enabling any grouse to dig itself into the snow within a matter of seconds. Snow-burrows serve as thermal refuges where birds may spend most of the day during hard frost and where the temperature is constantly around −2 to −3 °C regardless of the ambient temperature. The very fact that lateral pectination of the toes is not found in any other avian taxon significantly increases the taxonomic value of this feature. Similar structures are found in some desert lizards inhabiting loose sand (e.g. *Phrynocephalus, Eremias*) (Buxton 1928), but these are not homologues of grouse pectination, but rather transformed scales.

Feathering of nostrils and toes

Another characteristic feature of grouse is the full and thick feathering of the nostrils and, perhaps as a consequence, the complete absence of the horny covering flap, the operculum; in some members of the Phasianidae (e.g. *Lerwa lerwa, Tragopan, Lophophorus, Tetraogallus*) there is some feathering around and on the surface of the operculum, but the operculum itself is not reduced.

In most grouse the tarsi are thickly feathered apart from a narrow strip along the rear side. The great majority also have lateral feathering extended to the base of the toes; in *Lagopus*, the toes are completely feathered, except for the upper part of the extreme tips. Many phasianids, especially northern or mountain species, have feathering on the upper part of the tarsus, but never extended to the lower third, still less to the toes.

Skeleton

Among special features of the skeleton, the most notable is the great width of the pelvis—more than 75% of its length (in phasianids, the maximum width is up to 75.8%), while its depth is only 16–17% of its length (as against 25–30% in phasianids). Such a sharp increase in pelvic width has resulted in a characteristic bend in the femur which in turn brings about a shift in the centre of gravity to place it above the foot when walking.

Musculature

There are no qualitative distinctions between the groups being compared, all are of a quantitative nature. The sole significant distinction—the absence in the grouse of the M. adductor digiti II (Hudson *et al.* 1959) has now lost its validity since the discovery that this muscle is lacking also in a phasianid, namely the Tibetan Snowcock (*Tetraogallus tibetanus*) (Morioka 1975).

Digestive system

One of the main features of the digestive system is the exceptionally strong development of the caeca in all grouse species, this being most pronounced in members of the genus *Lagopus*. The length of grouse caeca is directly correlated with the length of the winter season and its relative severity, even within different populations of a single species. Generally, the length of the 2 caeca in grouse varies from c. 60 to 139% of the length of the small and large intestine; in phasianids, this ratio is usually up to 50%, in a few extreme cases up to 64% (Potapov 1985).

Among other peculiarities of the digestive system we should mention the absence in grouse of the gall bladder, which is so characteristic of other members of the Galliformes.

Ecological characteristics

Most important in this context as the main distinction from the phasianids is the peculiar food and feeding behaviour of grouse—their unique ability to survive on a monotonous plant diet throughout the severe winter season. Food items include twigs, buds, catkins and needles of various deciduous and coniferous trees and shrubs (e.g. *Betula, Alnus, Salix, Populus, Picea, Pinus, Abies*), i.e. a diet rich in cellulose and low in proteins and fats. However, food of this type is so abundant in northern forests that the birds need not spend much time or effort to obtain the required daily amount.

There are no fundamental differences between grouse and phasianids in respect of breeding strategy and timing (phenology), sex ratios, population dynamics, etc. The same general habitat types (open, bushy, forest, montane, etc.) are used by both groups, though grouse typically show a close link with forest and scrub vegetation and males of some species perform well-developed communal displays ('leks'). Open habitats invaded by grouse are primarily tundra (where some woody vegetation, even dwarf shrubs, is present), also to some extent steppe and semidesert, but never true desert. Grouse are found in all types of boreal forest, but have not penetrated into subtropical, still less tropical forests, the main reason being that their breeding range is confined within an area where there is a seasonal climate, with a pronounced winter period (snow cover, negative temperatures, short days).

Behavioural characteristics

The most remarkable feature of grouse behaviour is their ability to build snow-burrows as thermal refuges. For nocturnal or diurnal roosting, a bird uses vigorous movements of its bill and feet to dig a tunnel from 0.6 to 4 m long, at the end of which it makes a roosting chamber large enough to accommodate the bird comfortably, even with its feathers ruffled (Fig. 2). The depth of the chamber allows the grouse to stretch up and poke its head through the snow and look around before leaving its roost-hole. At moderate negative temperatures (minus 5 °C to minus 9 °C), grouse spend all the winter night in their burrows (Fig. 3),

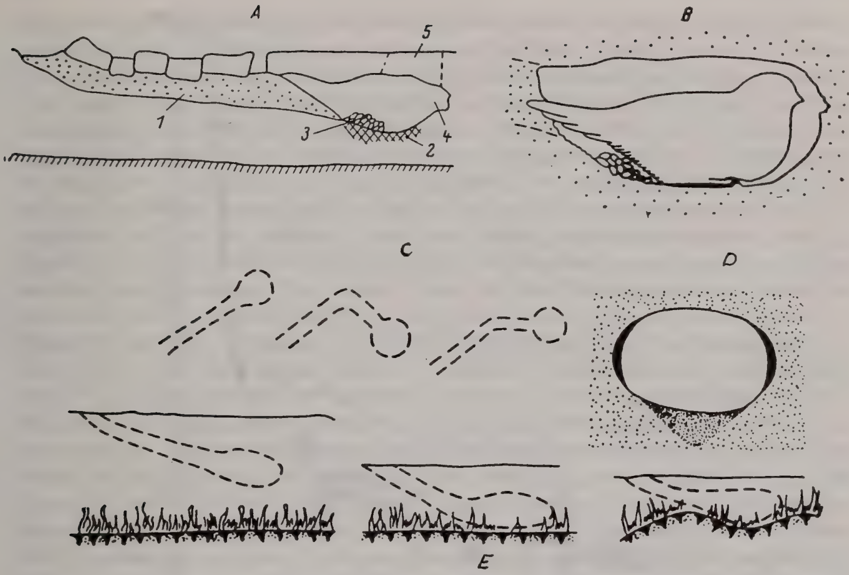


Figure 2. **Snow-burrow of grouse. A** = vertical cross-section of chamber; 1 = tunnel blocked with snow; 2 = platform of slightly thawed and compacted snow; 3 = solid faeces; 4 = signs of snow being eaten by bird; 5 = future exit hole. **B** = position of bird in burrow. **C** = various types of tunnels. **D** = transverse cross-section of burrow (black indicates icing of walls, shaded area shows platform of slightly thawed and compacted snow). **E** = position of burrow at varying snow depths. (From Potapov 1985).

and if the temperature is lower, all night and most of the day as well. In exceptionally low temperatures, a grouse can spend up to 22 hours per day or even more than 2 days in succession in its snow-burrow roost.

Functional significance of the above-mentioned peculiarities

All the characteristic features of grouse described above are directly or indirectly related to survival in the northern winter season and represent a highly effective complex of adaptations which allow the birds to be year-round residents, with no recourse to migration. This complex of adaptations is based on the ability to survive the winter on plant food of low nutritional value, but available in abundance and at low cost in both time and energy. In its turn, this ability is based on the presence of well-developed caeca into which passes all the liquid digestive extract (chyme) containing the main nutritionally valuable substances (fat, protein, micro-elements), also some less useful, even poisonous, substances, extracted from buds, twigs, needles, etc. during the grinding process in the gizzard and their passage through the digestive tract. In the caeca, the extract undergoes treatment for not less than 24 hours (usually nearer 48 hours per portion), thus significantly prolonging the digestive process; otherwise, the passage of food through the alimentary canal without this delay in the caeca takes c. 4 hours. The chemistry of the

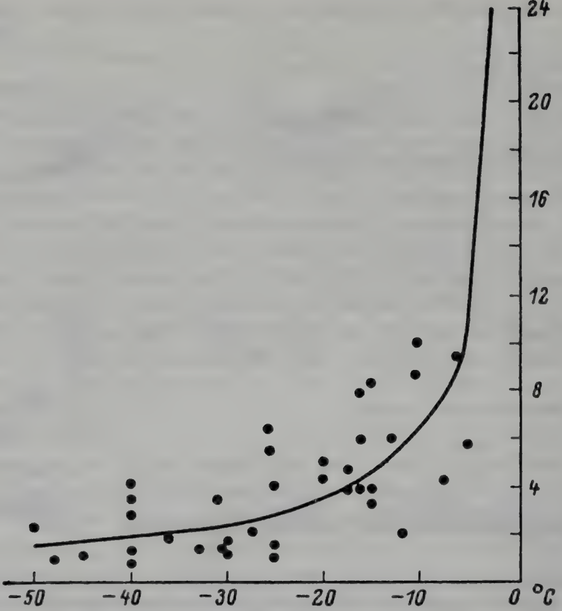


Figure 3. Time (Y-axis) spent outside the snow-burrow plotted against ambient temperature (X-axis). (From Potapov 1985.)

digestive process in the caeca requires further research; nevertheless, the caeca have been found to have intensive secretory activity with an exceptionally well-developed absorbent surface of their epithelium, the area and efficiency of which are considerably increased by the existence of well-developed ridges extending along the caeca. The caeca are thus a special kind of reactor working uninterruptedly throughout the winter to provide the bird with a constant supply of energy and nutrients.

It is on this main adaptation that all the other characteristic adaptations of tetraonid birds are based. They are able to survive on a diet of twigs, buds, catkins and conifer needles, i.e. items which are abundant and easy to obtain so that a minimum of time (30–90 minutes) needs to be devoted to gathering the daily ration. They have the ability to create thermal refuges under the snow which allow birds to regulate the ambient temperature by varying the time they spend in the burrow, which depends on the temperature outside. As a rule, the temperature in snow-burrows stays within optimal limits, just below 0 °C, and can even be regulated by the bird: if the temperature in the burrow rises above 0 °C and there is a consequent danger of the snow melting and the bird's plumage becoming wet, the grouse makes a small ventilation hole in the roof and the temperature in the burrow quickly drops. The thick feathering around the nostrils condenses moisture from the air exhaled by the bird, thus preventing the walls of the chamber icing up and an oxygen shortage arising. Any moisture is extracted from the faeces during their passage through the large intestine so that they are solid and dry when excreted and add some warmth to the air in the snow-burrow, while also to some extent absorbing unwanted moisture and thus helping to counteract the danger of icing. The bird's thick tarsal feathering is a superb thermo-isolating mechanism, giving a protective mattress against the cold floor. The harder the frost, the drier the snow and the better its insulating quality. If a thaw sets in, the snow becomes wet and unsuitable for roosting, but the grouse anyway no longer has a need for such a refuge once the temperature is 0 °C or above. In general, staying in a burrow during low temperatures leads to a great saving in energy thanks to a sharp reduction in energy expenditure on thermoregulation (the lower limit of the thermoneutral zone for tetraonid birds is close to 0 °C) and the virtually complete absence of locomotion. The decrease in energy expediture for thermoregulation alone, even in a moderate frost of −20 °C, means that a grouse uses 20–35% less of the energy required to survive at the given temperature otherwise than in a snow-burrow. It is not surprising, therefore, that the strategically important adaptation of making snow-holes has led to the evolution of certain morphological features which so sharply distinguish grouse from the other Galliformes: pectinated toes, which greatly increase the digging ability of the feet when burrowing into snow; thick feathering around the nostrils which protects them from snow and reduces moisture produced by condensation of the exhaled breath; and thick tarsal feathering (extending to the toes in some species) which acts as an insulating layer between the bird's body and the floor of the snow-burrow.

Conclusions

The above descriptions present a general picture of how the whole complex of adaptations peculiar to grouse operates. These adaptations function only during the winter and enable birds to lead a sedentary life despite the marked seasonality of the climate. Gallinaceous birds have, through representatives of the grouse, colonized a completely new natural zone which came into being and evolved during the last geological epoch (the Pleistocene). This is the zone dominated by the boreal tree-shrub vegetation-type (both deciduous and coniferous), which is in turn well adapted to sharp seasonal changes in climate. The enormous area occupied by this zone embraces practically all the land surface of the Northern Hemisphere north of latitude 40 °N. In other words, the grouse occupy at least 40% of the whole range occupied by gallinaceous birds. For the relatively ancient Galliformes (Eocene epoch), the whole of the boreal zone was completely new, as the order had evolved in the tropics and subtropics and only a few representatives of families other than grouse eventually managed to pentrate into the southern margins of the boreal forest zone. In this connection, we should bear in mind the generally accepted principle that the wider the new adaptive zone, the higher the taxonomic rank of a group by the time it occupies the greatest part of the zone in question (Simpson 1969). All these reasons should encourage us to regard the grouse as a separate family within the suborder Phasianoidea.

All large taxa within this suborder (pheasants, partridges, New and Old World quails, peafowl, guineafowl, turkeys and grouse) differ one from another to varying degrees in a number of mainly morphological features and this doubtless reflects the complex structure of the suborder and varying speed of evolutionary processes. Qualitatively and quantitatively the most distinctive groups are the grouse and guineafowl. However, while the grouse have predominantly new evolutionary features, the guineafowl are a distinctly archaic group. It is quite possible that the guineafowl also merit separation as an independent, but extremely primitive family, approaching in a number of morphological features, the suborder Cracoidea (Sych 1990).

Deserving of special attention are the New World quails whose morphology has not allowed taxonomic rank higher than subfamily within the Phasianidae. However, DNA-hybridization data have demonstrated that this group separated from the main branch of phasianids 35–65 million years ago, and should therefore be given family rank (Sibley & Ahlquist 1990, Sibley & Monroe 1990). It should be noted, incidentally, that determining the time when the New World quails diverged from the other phasianids can be done without recourse to the DNA-hybridization method, but instead by using palaeogeographical data from the time when the European and American continents separated. The DNA-hybridization results merely show the divergence of the chromosome structures; but in the present case it is clear that there is no corresponding divergence in the morphology of the groups being compared. This kind of dichotomy is by no means rare, having arisen regularly in recent times. In the case under investigation, it is my firm conviction that preference should be given to a judgement based on morphological criteria as these most convincingly show the results of the process of evolution. In assessing the taxonomic level of grouse, we therefore give higher priority to morphological features, their adaptive (functional) significance and specificity of ecological niches. On this basis, the relatively young, but morphologically and ecologically distinct grouse undoubtedly merit family rank within a superorder Phasiani, while the much older New World quails, which show no significant distinctions from the partridge and quails of the Old World (despite having separated millions of years ago), should be treated as a subfamily within the Phasianidae. The guineafowl, which are also younger than the ·New World quails, but (unlike grouse) are distinguished by their predominantly archaic features, suggesting a close relationship with the suborder Cracoidea, should evidently also be given family rank (Sych 1990).

The results of the process of evolution are not dependent simply on time, nor is taxonomic rank a mere function of time; it can be determined only after a detailed and comprehensive investigation of morphological, ecological and ethological features.

Acknowledgements

I am grateful to Michael G. Wilson (Edward Grey Institute, Oxford) for improving the language of the paper and also to M. & E. Potapov for typing the manuscript.

References:

Buxton, P. A. 1928. *Animal Life in Deserts*. London.

Clark, G. A. Jr. 1960. Notes on the embryology and evolution of the Megapodes (Aves: Galliformes). *Postilla* 45.

— 1964. Ontogeny and evolution of the Megapodes (Aves: Galliformes). *Postilla* 78.

Gutiérrez, R. J., Zink, R. M. & Edwards, G. D. 1983. Genetic variation, systematic, and biogeographic relationships of some galliform birds. *Auk* 100: 33–47.

Hudson, G. E., Lanzillotti, P. J. & Edwards, G. D. 1959. Muscles of the pelvic limb in galliform birds. *Amer. Midl. Nat.* 61: 1–67.

Morioka, H. 1975. Toe extensors and flexors of Tibetan Snowcock. *Bul. Natn. Sci. Mus. Ser. A. (Zool)* 1(2): 123–135.

Potapov, R. L. 1985. *Fauna of the USSR* N.S. No. 133, Birds 3(1). Order Galliformes, Part 2 Family Tetraonidae. Leningrad. (Russian).

Sibley, C. G. & Ahlquist, J. E. 1990. *Phylogeny and Classification of Birds*. New Haven, Connecticut.

Sibley, C. G. & Monroe, B. L. Jr. 1990. *Distribution and Taxonomy of Birds of the World*. New Haven, Connecticut.

Simpson, G. G. 1969. *The Major Features of Evolution*. New York.

Sych, V. F. 1990. *Morphology of the Locomotory Apparatus of Galliform Birds*. Doct. Thesis, Kazan' University.

Address: Prof. Roald L. Potapov, Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St Petersburg 199034, Russia.

© British Ornithologists' Club 1992

Reflections on the genus in ornithology

by Karel H. Voous

Received 20 March 1992

In the biologist's every day life, the use of a genus name is inevitable if not compulsory. Whether he studies the protozoan *Entamoeba*, the mosquitoes *Culex* or *Anopheles*, the herring *Clupea*, the Great Tit *Parus* or man himself *Homo*, for him the genus-name is significant if not decisive. He rarely ponders on what a genus actually means as a concept in systematic biology. Indeed, in most instances this is of no relevance to him. However, he may suddenly become painfully aware of it when taxonomists start to arrange the species of his study according to revised ideas of generic grouping. Worse still, he may see the familiar genus-name changed.

Almost 30 years ago I tried to formulate my thoughts on the essence of the genus in a Dutch journal (Voous 1964). Some time later I explained these in another paper written in English (Voous 1975), adding remarks on the theoretical and practical limits of genera in the warblers *Acrocephalus* and *Hippolais*, the gulls *Larus* and terns *Sterna*, and the geese *Anser* and *Branta*. The main conclusions were that, in contrast to species, genera have no reality in nature, that genera should be defined pragmatically and that non-taxonomic biologists are primarily interested in genus-names rather than in the genus itself. *Mutatis mutandis* this would apply to all other systematic categories above the species level. Only at the higher end, towards the category of the phylum, diversity in ontogeny and structure shows differences in principle rather than degree.

Introductory considerations

Renewed interest in the genus was induced by the publication of 2 important ornithological works, both of which have made important and markedly bold attempts to group the species of the birds of the world according to modern views and methods: Hans E. Wolters (†1991), *Die Vogelarten der Erde* (1975–1982), and Charles G. Sibley & B.L. Monroe, Jr., *Distribution and Taxonomy of Birds of the World* (1990).

Wolters announced himself as a strict follower of W. Hennig's phylogenetic systematics (Hennig 1950, 1966). Sibley & Monroe, though also following Hennig's principles of cladistic analysis, constructed a gigantic new building of bird systematics, based on the corner stones of DNA-studies. As was to be expected, Wolters's and Sibley & Monroe's classifications are as different *inter se* as each of these is from the traditional Wetmore system and its modifications.

Though of little relevance here, I have always had my own serious doubts as to the significance of Hennigian methods in taxonomy (Voous 1980, concurred with by Mayr 1982; 226–233). Whether viewed as a branching tree up to the finest twigs and end buds, or as a pruned bunch of grapes in which the pruning is executed by all natural phenomena in existence, the growth of certain twigs or grapes are favoured, while others lead to extinction or radical pruning. The result is that the tree of life formed by both transient and recent species is far too complicated and too incompletely known, if known at all, so that the recognition of branching points, as required by Hennig, involves too many basic uncertainties as to be of any real help in understanding the road of evolution. When making a choice out of a multitude of possible options for the reconstruction of a phylogenetic tree, the word "parsimonious" emerges as of having magical power. I must confess that, English not being my mother's tongue, I have met this word only in Hennigian contexts and I am not impressed by it. As every experienced biologist knows, nature's ways are, and probably always have been, more capricious and unpredictable than man can encompass. Hence, all Hennigian-derived phylogenetic trees are theories, not necessarily better or nearer to reality than any other serious endeavour to reconstruct the past. Trying to discriminate between 'apomorphic', 'plesiomorphic' and other categories of characters, which is another important item in Hennigian methodology, is as subjective a procedure as it was to distinguish between homologous and analogous characters or structures in old-fashioned comparative anatomy, which therefore ultimately failed.

With this in mind and passing by the several published theoretical observations on the genus concept, I have ventured to evaluate the use of genera in the comprehensive works of Wolters (1975–1982) and Sibley & Monroe (1990). The results of the evaluation will be compared with the conclusions arrived at in earlier papers (Voous 1964, 1975).

Comparing the uses made of genera in avifaunal lists

In order to evaluate the genus concepts adhered to by Wolters (1975–1982) and Sibley & Monroe (1990) I have compared the genus-names accepted in these works with those used in:

(1) New World breeding birds, as in the A.O.U. *Check-list of North American Birds* (6th ed., 1983): Nearctic region only.

(2) Old World breeding birds, as in the *List of Recent Holarctic Bird Species* (Voous 1973, 1977): Europe only.

(3) Tropical Asiatic birds, as in *The Birds of Sumatra* (van Marle & Voous 1988): breeding birds of Sumatra and satellite islands.

As stated before, Wolters has tried to apply cladistic methods at every taxonomic level, including that of subgenera. Hence his classification differs from that of any of his predecessors. The actual reasoning behind each individual case is not explained, but the reader is referred to an earlier paper on the limits of genera in ornithology in general (Wolters 1971). As a result Wolters lists no less than 356 (289) genera in North America, 270 (213) genera in Europe, and 281 (220) genera in Sumatra (traditional numbers added in parentheses).

In contrast, Sibley & Monroe have been wise enough to lay the stress on their truly revolutionary arrangement and sequence of higher taxonomic categories, viz. tribe, family, infraorder, suborder, order, parvclass, infraclass, subclass. They have rarely deviated from the traditional path in the extent and limits of genera and the use of genus-names. This is all the more pleasurable since the names and their meaning in taxonomy will be recognised by ornithologists and biologsts of any discipline. Actually, their basically quantitative biochemical methods would have hardly left them room for deciding otherwise. Sibley & Monroe list 291 (289) genera in North America, 212 (213) genera in Europe, and 226 (220) genera in Sumatra (traditional numbers added in parentheses).

Fortunately, Wolters and Sibley & Monroe concur in as many as 24 instances, listed below, in which they deviate from one or more of the traditional classifications with which their works were compared:

Morus (not *Sula*) *bassanus*
Ixobrychus (not *Dupetor*) *flavicollis*
Nyctanassa (not *Nycticorax*) *violacea*
Casmerodius (not *Egretta*) *albus*
Mergellus (not *Mergus*) *albellus*
Asturina (not *Buteo*) *nitida*
Porphyrio (not *Porphyrula*) *martinica*
Burhinus (not *Esacus*) *magnirostris*
Eudromias (not *Charadrius*) *morinellus*
Micropalama (not *Calidris*) *himantopus*
Steganopus (not *Phalaropus*) *tricolor*
Larus (not *Xema*) *sabini*
Rhaphidura (not *Chaetura*) *leucopygialis*
Tachymarptis (not *Apus*) *melba*
Todiramphus (not *Halcyon*) *chloris*
Actenoides (not *Halcyon*) *concretus*
Tricholestes (not *Hypsipetes*) *criniger*
Iole olivacea (not *Hypsipetes charlottae*)
Ixos (not *Hypsipetes*) *malaccensis*
Hemixos (not *Hypsipetes*) *flavala*
Eumyias (not *Muscicapa*) *thalassima*
Eumyias (not *Muscicapa*) *indigo*
Psilorhinus (not *Cyanocorax*) *morio*
Hesperiphona (not *Coccothraustes*) *vespertina*

Case studies

Anatidae: swans, geese, ducks

The number of genera recognized by Wolters is 72, by Sibley & Monroe 44, average number of species per genus 2 and 4, respectively. Recognising 13 genera of surface-feeding or dabbling or paddling ducks by Wolters, instead of the one genus *Anas* by Sibley & Monroe, means in terms of cladistic analysis that Wolters's first genus, "*Melananas*" for the African Black Duck *Anas sparsa*, is the 'sister-group' of all following genera combined. It is hard to believe that evidence in favour of this suggestion is available, nor that the 3 species of wigeon '*Mareca*', following '*Melananas*' have subsequently together branched off from the main and only stem from which in later times all other *Anas*-ducks have derived. The scholarly ecological studies by Johnsgard (1965) on which Voous (1973) and others have based their sequence of ducks, would not suffice for that purpose, as nothing is known of the real history of the evolution of these ducks.

Curiously enough, the delimitation of these duck-genera by Wolters conforms almost exactly with the genera recognised in older European works and perpetuated still in the 4th edition of the A.O.U. *Check-list* of North-American Birds (1931) in which *Anas* is split into 9 genera: *Anas, Chaulelasmus, Dafila, Paecilonetta, Eunetta, Nettion, Querquedula, Mareca* and *Spatula*. Morphological differences (e.g. in the structure of the bill, corresponding with feeding habits and habitats) formed the background for recognising these groups as genera. So we are back to where taxonomy started: comparative morphology, as a subjective, but verifiable basis for genus-recognition, now in modern Hennigian disguise. Realising that this is the position of a modern classification does not mean yielding to scientific incapacity, but is merely to put the record straight.

Using 50 (Wolters) or 35 (Sibley & Monroe) genera for all 40–42 duck species together, signifies differences in taxonomic view and treatment, but one method is scientifically not more acceptable than the other. For the general ornithologist, however, a restricted number of genus-names reflects the situation more clearly that the similarity of duck species in appearance and behaviour is more apparent than the difference. Besides, in spite of differences in male breeding attire, these birds are genetically remarkably closely related as testified by the occurrence of the most extravagant, and often fertile, hybrid combinations, occurring as well in captivity as in nature; and was it not the possibility of producing fertile hybrids that was considered the crucial condition for recognising "wide" genera in Wolters's earlier writings (Wolters 1949, 1950)?

Falconidae: falcons

The number of genera of falcons recognised by Wolters is 10, by Sibley & Monroe one, average number of species per genus 4 and 39, respectively. Admittedly, there are marked differences between the 'inoffensive' kestrels '*Tinnunculus*' and the 'fierce' gyrfalcons and peregrines '*Hierofalco*'. If the use of the one genus-name *Falco* for all falcons is considered unsatisfactory because of the differences between the extremes, the splitting up of the genus could be considered a remedy. This would leave Merlin '*Aesalon*', Hobby '*Falco*' and Eleonora's Falcon '*Falco*' in intermediate positions and would place the Red-footed Falcon '*Erythropus*' on a specialised side-branch. Still, the history of the evolution of falcons is virtually unknown. For the use of a variety of genus-names for the falcons, nothing but the old-fashioned method of weighted phenological taxonomy remains in stock. Trying to find 'sister-groups' in this and comparable cases is unrealistic, and Hennigian methods fail or are at best as subjective as any other method.

Calidridinae (Eroliinae): sandpipers

The number of genera recognised by Wolters is 11, by Sibley & Monroe 6, average number of species per genus 2 and 4, respectively. Basically the same considerations as in the case of the *Anas*-ducks could apply to the use of genus-names in this group of waders which, as in ducks, look so much alike and behave so similarly *inter se*, yet in some respects can be so markedly different. Subjective comparative morphology rather than the reconstruction of branching points in their long line of evolution has provided the basis for the recognition of the genera *Calidris* (Knot), *Erolia* (Curlew Sandpiper), *Heteropygia* (Pectoral Sandpiper), *Ereunetes*

(Semipalmated Sandpiper), *Crocethia* (Sanderling), *Pelidna* (Dunlin), *Arquatella* (Purple Sandpiper). They are distinguishable mainly on account of one or two vestigial webs at the base of toes and the absence, presence or size of the hind toe, none of which characters seem to play a major specific role in sandpipers' lives. Apart from weak scientific evidence, a profusion of genus-names more likely conceals than elucidates the degrees of relationship in these waders.

Laridae: gulls

The number of genera of gulls recognised by Wolters is 12, by Sibley 6, average number of species per genus 4 and 8, respectively. In a former paper (Voous 1975) I have tried to show that a wide genus *Larus*, including such extremes as the Great Black-backed Gull *Larus marinus* and Little Gull *Larus minutus* is consistent with the facts only when in the related terns a similarly wide genus concept is accepted. It was therefore proposed to list the Caspian Tern (*caspia*) and the Little Tern (*albifrons*) and all terns in between as members of one genus *Sterna*. The alternative view is to have these 2 genera divided into several, which is what Wolters has done. Apart from the Kittiwake *Rissa* and the Ivory Gull *Pagophila*, all 'white-headed' gulls, from Common Gull (*canus*) to Great Black-backed (*marinus*) and Glaucous (*hyperboreus*) Gulls are listed by Wolters as *Larus*, as opposed to the ''hooded' gulls, which are arranged in as many as 7 genera: *Adelarus* (Hemprich's or Aden Gull, 2 species), *Ichthyaetus* (Great Black-headed Gull, 1 species), *Chroicocephalus* (Black-headed Gull, 13 species), *Atricilla* (Laughing Gull, 3 species), *Hydrocoelus* (Little Gull, 1 species), *Rhodostethia* (Ross's Gull, 1 species) and *Xema* (Sabine's Gull, 2 species). Even a detailed cladistic background for this classification cannot provide the real evolutionary history which has brought about the present wealth of gull species, disclosing the subjective nature of this arrangement. Apart from that, the question remains whether one considers it more practical and helpful to adhere to one, well-defined large genus or alternatively should accept a number of less clearly defined smaller genera. Obviously, most present authors opt for the least amount of genus splitting.

Concluding remarks

The practicability and direct understanding of the limits of genera and of genus-names are the most relevant, and at the same time most widely appreciated, requirements for the genus, at least in ornithology. Most authors agree on the fact that whenever possible the genus should include a monophyletic group of species distinct from other such monophyletic groups. In most cases, in the absence of palaeontological data, the reality of a monophyletic origin of an individual genus cannot be or has not yet been proved. Hennigian analysis has not improved this situation. Real though the clustering of species is in evolutionary history, the reality and even the meaning of genus-limits are questionable. Genus-names remain as auxiliary help for understanding and memorising classification systems and in this respect are useful for any kind of ornithological research. Pragmatic rather than scientific values should be attached to bird genera and their naming.

In addition some of my earlier conclusions seem to have remained valid: (1) species, as functions of time and place, are a reality in nature; (2) genera are abstractions and as such do not exist in nature; (3) species can be discovered in nature, genera cannot; genera are invented (Voous 1964); (4) evolutionary development is gradual; in contrast, the distinction of genera is discontinuous by its very nature; (5) the recognition of genera should not be considered a necessary means of expressing evolutionary relationships, a presumption which after all is an unwelcome heritage of 19th century thinking; (6) "The choice in the use of [named] genera should be practised according to the same standards as [for] literary style and with the same . . . elegance and precision, combining the subtilities of art with the [rigid] abilities of science" (Voous 1975: 982).

References:
American Ornithologists' Union. 1931. *Check-list of North American Birds*. 4th ed. American Ornithologists' Union. 1983 6th ed. Lawrence, Kansas: Allen Press.
Hennig, W. 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin: Deutscher Zentralverlag.
— 1966. *Phylogenetic Systematics*. Urbana, Illinois: Univ. Illinois Press.
Johnsgard, P. A. 1965. *Handbook of Waterfowl Behaviour*. London: Constable.
Marle, J. G. van & Voous, K. H., 1988. *The Birds of Sumatra*. British Ornithologists' Union Check-list No. 10. Zoological Museum, Tring, Herts, UK.
Mayr, E. 1982. *The Growth of Biological Thought*. Cambridge, Mass. and London: Bellknap of Harvard Univ. Press.
Sibley, C. G. & Monroe, B. L., Jr. 1990. *Distribution and Taxonomy of Birds of the World*. New Haven: Yale Univ. Press.
Voous, K. H. 1964. Het genusbegrip in de zoölogie in theorie en praktijk. *Vakblad Biol.* 44: 139–149.
— 1973. List of recent holarctic bird species. Non-Passerines. *Ibis* 115: 612–638.
— 1975. An aberrant Reed Warbler, or: on the inequality of genera in birds. *Ardeola* 21: 977–985.
— 1977. List of recent holarctic bird species. Passerines. *Ibis* 119: 223–250, 376–406.
— 1980. New developments in avian systematics: a summary of results. *Acta XVII Congr. Int. Orn.* Berlin (1978): 1232–1234.
Wolters, H. E. 1949. *Beiträge zur Gattungssystematik der Vögel*. Krefeld:: Goecke & Evers.
— 1950. *Beiträge zur Gattungssystematik der Vögel*. II. Krefeld: Goecke & Evers.
— 1971. Probleme der Gattungsbegrenzung in der Ornithologie. *Bonn. Zool. Beitr.* 22: 210–219.
— 1975–1982. *Die Vogelarten der Erde*. Berlin: Parey.

Address: Professor Dr. K. H. Voous, Maasdamlaan 28, 1272 EM Huizen, The Netherlands

© British Ornithologists' Club 1992

New species of birds described from 1981 to 1990

by *François Vuilleumier, Mary LeCroy & Ernst Mayr*

Received 28 May 1992

At the VIIIth International Ornithological Congress in Oxford, Meise (1934) presented a detailed review of avian taxa described as new in the 15 year period from 1920 to 1934. No fewer than 600 new *binomina* were described in those 15 years. Meise (1934: 61) thought that "at least 135, at most 170–200 [of these 600 proposed species were] good species". This represents a rate of 40 new species names per year, and from 9–13 'good' new species per year. Four years later, at the IXth International Ornithological Congress in Rouen, Meise (1938) presented "not only the species of birds described since July 1934, but also most of the species described between 1920 and 1934, which had not been presented in London in 1934." He included 59 species names, 36 of which were described between 1920 and 1934. This left 23 new species described from 1935 to 1938, a rate of about 6 new species per year. Much less detailed than the 1934 paper, the 1938 one simply listed the new names for the 1934–1938 period and the supplement for 1920–1934. The 1934 paper included the new species in a systematic order and grouped them by major regions as well: North and South America; Africa, Madagascar and southern Arabia; Palaearctic Region; Indomalayan Region; Indo-australian Mixed Region; and Papuan Region and Polynesia. It gave a critical evaluation of the new names (Meise 1938), and placed them in a number of categories, including: "I. Recognized as a species"; "II. Recognized as subspecies"; "III. Homonym"; "IV. Synonym" (with several subcategories); and "V. Not recognized". By contrast, the 1938 list (Meise 1938) only gave the species names grouped in geographic order. Meise (1938) indicated that the list "did not correspond to all described species" and that "several species must rather be considered as subspecies"; but no specific annotations were made.

From the World War II years onward, the responsibility for periodic reviews of new avian species has been assumed by members of the scientific staff of the Department of Ornithology at the American Museum of Natural History (AMNH), most notably Ernst Mayr. Thus the 4-year period 1938–1941 (53 putative new species) was covered in the first AMNH review (Zimmer & Mayr 1943). The second (Mayr 1957) covered the 15-year period from 1941 to 1955 (74 putative new species), the third (Mayr 1971) the 10-year period from 1956 to 1965 (51 putative new species). The fourth instalment (Mayr & Vuilleumier 1983) reviewed critically the 48 species described as new in the 10 years between 1966 and 1975, and the fifth instalment (Vuilleumier & Mayr 1987) discussed the 18 species described as new in the 5-year period from 1976 to 1980, plus one species that had been omitted from the fourth report.

The present article is therefore the sixth AMNH instalment. It covers the 43 new species of birds that have been described between 1981 and

1990 (listed alphabetically in Appendix I), thus bringing the analysis up to date. The present report also reviews 3 species that had been overlooked in the compilation of previous reports (Appendix II), discusses 2 taxa that have been described as potential new species in the period 1981–1990 but that were not given *binomina* (Appendix III), and makes comments on 13 species discussed in previous reports, and for which information is very scanty (Appendix IV). As in the last instalment, species are grouped under 2 headings: Old World and New World. Within each region, the systematic order of families and subfamilies follows Morony *et al.* (1975).

This review, as the earlier ones, provides ornithologists with a critical summary of information on bird species described as new in the literature. After a study of the available evidence, each putative new species is ranked in one of several categories. To facilitate comparisons these categories are the same as in previous instalments in this series:

Aa	New species in new genera
Ab	New species not clearly members of a superspecies
Ac	Allospecies (members of a superspecies)
Ba	*Species inquirendae*
Bb	Subspecies
Bc	Synonyms
Bd	Invalid names

As in our earlier reports superspecies are indicated by brackets according to the procedures suggest by Amadon (1966).

While preparing this review we have noticed that there is an unhealthy disease striking some ornithologists at present, aptly named "new-species fever" by Remsen (*in litt*). They seem impelled to describe as new a bird that seems to differ from a known species without collecting the data and making the careful studies that are necessary for an evaluation of relationships. General ornithological or natural history magazines (e.g. *Ducks Unlimited, Animal Kingdom, Ornis, BBC Wildlife, World Birdwatch, American Birds, Der Falke*, and others) and science journals (e.g. *Nature*) often carry popular articles about putative new species of birds, and recently a book (Stap 1990) recounted the search for novelties in the jungles of Amazonia. In several instances, putative new species have prematurely been incorporated into field guides (e.g. *Diomedea amsterdamensis* in Harrison 1985; *Calidris paramelanotos* in Hayman *et al.* 1986). We have attempted, in this summary, to bring together this scattered literature of varying quality as well as material from the standard ornithological literature and present a coherent evaluation of each new species.

In addition, we have become concerned at the careless way in which the descriptions of new species are sometimes presented. Evaluation is difficult when descriptions are based on fragmentary data. Two of us (LeCroy & Vuilleumier 1990) presented a poster paper at the XXth International Ornithological Congress in New Zealand, making recommendations for criteria to be used in describing new species of birds. We have expanded these suggestions and publish them as a separate paper in this volume.

We reiterate a request made earlier (Vuilleumier & Mayr 1987) and ask that ornithologists who describe new species send us copies of their papers, to facilitate our task in the future, and to ensure the continuity of this catalogue, which we believe has proven helpful to the ornithological community. General reviews making use of instalments in this series include Vuilleumier (1976) and Prigogine (1985).

New taxa of subfossil birds (e.g. *Dromaius baudinianus*—Parker 1984 and *Ara cubensis*—Wetherbee 1985) are not treated in this paper, which deals only with extant taxa.

OLD WORLD

Diomedeidae

(1) *Diomedea amsterdamensis* Roux, Jouventin, Mougin, Stahl & Weimerskirch 1983, *L'Oiseau et R. F. O.* 53: 8—Plateau des Tourbières, Amsterdam Island 37°50′S, 77°35′W, Indian Ocean.
=*Diomedea (exulans) amsterdamensis* (Bb).

The head and wing of a bird found dead on 28 March 1982, preserved in the Muséum National d'Histoire Naturelle (MNHN) in Paris (C. G. 1982–1139) form the holotype of this new species. No additional specimens were collected owing to the threatened status of this taxon. The authors did not find any specimen of large albatross from the Amsterdam Island population in the collections of the MNHN (other than the holotype), the Natural History Museum (BMNH) in London, the American Museum of Natural History (AMNH), the Carnegie Museum in Pittsburgh, the National Museum of New Zealand, or the U.S. National Museum (USNM) in Washington.

Although the existence of a breeding population of a large albatross on Amsterdam Island has been known since 1951, very little was known about these birds until 1981, when 7 breeding pairs were found and their behaviour observed until the young fledged. The total population size, from data gathered in 1979, 1981 and 1982, is estimated at 30–50 individuals. The distribution of this population at sea is entirely unknown.

Diomedea amsterdamensis was described on the basis of field observations and photographs of 23 breeding adults, and is illustrated with line drawings and black and white photographs. This population is closely related to *D. exulans* and *D. epomophora*. *D amsterdamensis* differs from *D. exulans* and *D. epomophora* in its much darker colouration, in the dark terminal patch at the tip of the bill, in its white eyelid, in its underwing pattern, and in the timing of its breeding cycle. Roux *et al.* (1983) concluded (translated from the French): "The originality and the absence of variability in the colour characters of plumage and bill testify to the reproductive isolation of this population. Moreover, the phenology of its breeding cycle forbids [*interdit* in the original] any hybridization with the other populations of *D. exulans* and *D. epomophora*."

Bourne (1989: 110) reviewed the classification of the large albatrosses. He pointed out that *D. amsterdamensis* "appear[s] to be rather similar in size, proportions and appearance to the birds assigned to *exulans* from the Antipodes Islands in the Pacific". The white eyelid, Bourne (1989: 110) remarked, was thought to be "a variable character in Wandering Albatrosses" by Murphy (1936). Bourne (1989: 111–113) also warned of possible nomenclatural problems: "If it is accepted that Edwards' birds [from which Linnaeus described the species] probably came from Amsterdam Island, the well-known name *exulans* would take priority over *amsterdamensis*, while if it is accepted that this is a distinct species another name, *chionoptera*, would then have to be used for most of the other populations currently included in *Diomedea exulans*." Because of difficulties in determining the identity of the population described by Edwards, however, Bourne (1989) suggested that the Amsterdam Albatross be called *Diomedea exulans amsterdamensis*, an opinion we accept here, (Bb). In Bourne's (1989: 113) words, *amsterdamensis* is "a small pelagic form which retains the immature plumage into adult life". Sibley & Monroe (1990: 327) included *exulans* and *amsterdamensis* as allospecies in a superspecies. Some ornithologists (for instance Jouanin, pers. comm.) feel that *exulans, epomophora* and *amsterdamensis* are 3 species in the same subgenus. Others (e.g. Boles, *in litt.*) point out that some populations of *exulans* approach *amsterdamensis* in colour.

Jouventin *et al.* (1989) reviewed data on the breeding biology of the Amsterdam Island population of great albatross, and compared this population to others in the species *epomophora* and *exulans*. The size of the population at this later date was estimated to be about 65 birds (between a minimum of 52 and a maximum of 90). Lequette & Jouventin (1991) discussed behavioural similarities and differences among the different taxa of great albatrosses and described the displays of *Diomedea amsterdamensis*. They concluded that *D. epomophora* is "more distinct than the other two [species (*exulans* and *amsterdamensis*)] which nevertheless present some differences in their nuptial displays" (Lequette & Jouventin 1991: 391).

Given some of the uncertainties of classification of the great albatrosses (e.g. Bourne 1989, Lequette & Jouventin 1991), it is to be regretted that authors of field guides (e.g. Harrison 1985) should have hurried to include *amsterdamensis* as a new species without having had the benefit of prior critical assessment.

Rallidae

(2) *Rallus okinawae* Yamashina & Mano 1981, *J. Yamashina Inst. Ornith.* 13: 2—Woodland path near Mt. Fuenchiji, Kunigami-gun, Okinawa Prefecture, Japan.

= *Gallirallus [torquatus] okinawae* (Ac).

This new rail taxon, from the island of Okinawa, was not discovered until 1978. The holotype, an adult female, was found along the roadside on 2 June 1981, and is preserved in the Yamashina Institute for Ornithology (No. 810141). Two other birds, a juvenile captured 28 June 1981, and an (unsexed) adult caught 4 July 1981, were photographed, banded, and released. They are illustrated in 3 colour plates (from photographs) in Yamashina & Mano (1981). *Rallus okinawae* was compared to various taxa of the *torquatus* group (*torquatus, kuehni, celebensis, limarius,* and *sulcirostris*), and found to have longer tarsi. This, coupled with the short and "soft" secondaries and tail feathers, suggested to Yamashina & Mano (1981) that *okinawae* has "very poor" flying ability, and hence that it is "a distinct new species".

Brazil (1991: 111–112) summarizes what is now known of this bird. Its population, thought at first to be very small, is now believed to number between 1000 and 2000 birds. "It occurs in sub-tropical evergreen forests with dense undergrowth, but also along forest edges and in small forest patches, scrub and even agricultural land where it borders pools." The bird appears "almost, but not quite, completely flightless" (Brazil 1991: 112). Other information about habitat, breeding, behaviour and vocalization are given by Brazil (1991).

Rallus okinawae is clearly closely related to island rails of the *torquatus* group, including *insignis* from New Britain, and various forms occurring from the Philippines to Sulawesi (Celebes), the Moluccas and Irian Jaya (New Guinea). We consider (near) flightless *okinawae* to belong in the superspecies including *torquatus* (flying) and *insignis* (flightless) (category Ac), and placed by Olson (1973) in the genus *Gallirallus*, an opinion that is shared by White & Bruce (1986) and Sibley & Monroe (1990: 223). Diamond (1991) in his description of another new flightless species of *Gallirallus* from the Solomon Islands, discussed some problems of the independent evolution of flightlessness in island rails.

Given the healthy population size of *R. okinawae*, we hope that a small sample of specimens, including skins, skeletons and tissues, will be collected and deposited in major collections for further study.

Scolopacidae

(3) *Calidris paramelanotos* Parker 1982, *South Australian Naturalist* 56(4): 63—Price Saltfields, upper Gulf St. Vincent, South Australia.
= ? *Calidris paramelanotos* (Ba).

The holotype, collected 5 March 1977, and the paratype, collected 16 February 1985, are in the South Australian Museum (Parker 1982). The very short original description (not accompanied by illustration) stated that the Cox's Sandpiper *C. paramelanotos* "resembles the Pectoral Sandpiper *C. melanotos* in size, shape of tail and pigmentation of primary shafts". It was said to differ from *C. melanotos* in several characters, including bill length and bill colour, leg colour, colour of pectoral plumage, colour of rump feathers, and other plumage characters, including colour of the median upper tail-coverts. The original description gave no information of a nature such as to suggest that the 2 specimens (holotype and paratype) did, indeed, represent a new biological taxon in the genus *Calidris*. No mention was made of detailed comparisons with any other *Calidris*, save *C. melanotos* or of the possibility of hybridization.

Since the original observation of an unusual sandpiper in southern Australia by John B. Cox (1989a) and others, a veritable flood of literature has been pouring forth on this putative species. In an article by Cox, entitled "The story behind the naming of Cox's Sandpiper" (1989b), the author "seeks to clarify the . . . controversy . . . that has become an embarrassment to Australian ornithology". We will not review here this enormous literature, other than to note that little of it has appeared in *serious* scientific ornithological journals, but instead refer to a short piece by Monroe (1991), who listed the pertinent papers (*q.v.*) and who succinctly summarized much of the *evidence*. Several points need to be made: (1) There are 4 specimens; (2) "The breeding range is unknown"; (3) "The full alternate and juvenal plumages are also unknown"; (4) "All four specimens and most photographs . . . are intermediate in all characteristics between the Curlew Sandpiper (*C. ferruginea*) and the Pectoral Sandpiper (*C. melanotos*)"; (5) "It is hopeful that biochemical studies underway will resolve the issue with respect not only to the hybrid origin but also to the correct parentage" (Monroe 1991). See also Sibley & Monroe (1990: 240), who stated: "Present evidence is not sufficient to confirm or refute the hypothesis of valid species or that of hybrid origin".

Stepanyan (1990) suggested that *C. paramelanotos* is a hybrid between a male of either *C. acuminata* or *C. melanotos* and a female of *Philomachus pugnax* on the basis of morphological and behavioural characters. Furthermore, he suggested that the recent eastward range expansion of *P. pugnax* into the Chukotski Peninsula puts this species in sympatry with both *C. acuminata* and *C. melanotos*, hence the recency of the sudden appearance of *C. paramelanotos*. One of us (ML *in litt.* to Parker in 1978) suggested that if the birds are hybrids, "one parent might be *C. acuminata*".

For the time being, we suggest that *C. paramelanotos*, which is likely to be of hybrid origin, be maintained as a *species inquirenda* (category Ba).

We strongly feel that the inclusion of "*Calidris paramelanotos*" in a book such as *Shorebirds, an Identification Guide to the Waders of the World* (Hayman *et al.* 1986) is premature, given the lack of information on this putative new species.

Strigidae

(4) *Glaucidium albertinum* Prigogine 1983, *Rev. Zool. Afr.* 97(4): 887—Musangakye (1690 m.), Zaïre.
= ? *Glaucidium albertinum* (Ba).

Five specimens of pygmy owls collected between 1950 and 1981 in Zaïre and Rwanda formed the basis for the description of this new species. All 5 (including the type) are in the Koninklijk Museum voor Midden-Afrika (KMMA), Tervuren (holotype has number 114546). "*Glaucidium albertinum* is restricted to forests around the Graben (Albertine Rift) in Central Africa. Whereas the first two specimens came from transitional forest, the other three were found in mountain forest" (Prigogine 1983: 889). Two poorly reproduced black and white photographs showing dorsal patterns accompany the original description. Formerly confused with *G. castaneum*, the birds included in *G. albertinum* differ from *G. capense* in several characters, including the pattern of the head and back, the barred uppertail coverts, and the brown rather than rich chestnut colour. *G. albertinum* is more uniformly coloured on the back than is *G. castaneum*. *G. albertinum* has a shorter tail, and a lower wing/tail ratio than *G. castaneum* and various subspecies of *G. capense*. *G. albertinum* also has fewer bars on the central tail section (6–8, *versus* 9–10 in *G. castaneum*, and 10–11 or 13 in *G. capense*). Prigogine (1983: 892) concluded: "Taking into account the light barring on the back of *G. castaneum*, its barred uppertail coverts and its measurements, one must consider *castaneum* as a subspecies of *G. capense* which may form a superspecies with *G. albertinum*." No detailed information was given about the geographical relationships of these 3 taxa (*albertinum, capense* and *castaneum*). The voice of *albertinum* is unknown.

In a later paper, Prigogine (1985: 92) reviewed aspects of *G. albertinum* and confirmed its distinctness, based on morphological similarity among the 5 specimens, and morphological differences between them and *G. capense* and *G. castaneum*. (Small individual variation had been noted earlier—Prigogine 1983). In his Appendix (Table A.1, p. 106), Prigogine (1985) indicated the status of *G. albertinum* as '? species'. Keith (pers. comm.) believes *G. albertinum* to be a good species but that too little is known to ascribe it to a superspecies, especially since its voice is unknown. Sibley & Monroe (1990: 179) accept *G. albertinum* as a full species.

In view of the difficulties in the species-level systematics of owls in the genus *Glaucidium*, and given the absence of data on vocalizations and ranges, it seems impossible at present to decide whether *G. albertinum* is or is not an allospecies of *G. capense* or whether it is a *species inquirenda*. Given these uncertainties we conservatively rank it at present as Ba. Only further evidence will permit a decision to be made between these possibilities.

Caprimulgidae

(5) *Caprimulgus prigoginei* Louette 1990, *Ibis* 132: 349—Malenge, Itombwe, Kivu Province, Zaïre, at 03°26′S, 28°30′E; in forest at 1280 m altitude.

= *Caprimulgus prigoginei* (Ab).

This new species of nightjar (illustrated in a colour plate) was described on the basis of a single female specimen collected on 11 August 1955 by Prigogine's collector in the Itombwe forest in Zaïre. The holotype, number 78975 is deposited in the KMMA.

Chiefly on the basis of size, proportions, and colour pattern, Louette (1990) thought that this bird represented a new species which is not closely related to *Caprimulgus batesi*, with which it was thought to belong previously. After comparing this specimen with all species of African Caprimulgidae except *C. eximius*, Louette (1990: 349) concluded that "it does not belong to any of the known species from Africa" and added "Although only known from a singleton, the evidence amply justifies treating this distinctive nightjar as a new species". Louette (1990: 352) went so far as to state: "I have no hesitation in considering *C. prigoginei* to be a new species without close relatives among the known nightjars."

This new species is unknown in life. Louette (1990: 352) listed other bird species collected at the type locality in order to predict what the new nightjar's habitat might be.

Keith (pers. comm.) believes that *Caprimulgus prigoginei* is undoubtedly a good species because it does not resemble any African species of caprimulgid and it does not have any shared or intermediate characters that would cause one to suppose it might be a hybrid.

In view of the distinctiveness of this new species we classify it as Ab (new species not clearly a member of a superspecies). We hope that more museum specimens of this interesting new taxon will be discovered in the near future and that it can be studied in nature.

Indicatoridae

(6) *Melignomon eisentrauti* Louette 1981, *Rev. Zool. Afr.* 95(1): 131—c. 2 km east of Grassfield (7°30′N, 8°35′W), Mt. Nimba, Liberia.
= ? *Melignomon eisentrauti* (Ba).

This new species is based on 2 specimens. The holotype (a ♀ with an enlarged ovary) was collected in 1980 and is housed at the KMMA (No. 80-36-A-218). The paratype (also ♀) is in the State Museum of Natural History, Stuttgart, and was collected by M. Eisentraut in 1957 on Mt. Cameroon. The 2 specimens of *M. eisentrauti* were compared to a series of *M. zenkeri* from Zaïre. The original description includes very little comparative information and no illustrations. Apparently *M. zenkeri* is "much more greenish-yellow ventrally". A table includes only measurements of 20 *M. zenkeri*, which do not differ significantly from measurements of the type and paratype of *eisentrauti*. Louette (1981: 135) stated: "*M. eisentrauti* is likely to be allopatric of [*sic*] the Lower Guinean *zenkeri* and will almost certainly be found in other forest remnants between western Cameroon and Sierra Leone."

Colston (1981) published, nearly simultaneously, a paper on the same taxon, and wrote: "A copy of this paper, proposing a new name, was sent to Dr M. Louette in October 1980, shortly after it had been submitted for publication. Dr Louette has since seen fit to describe the new honeyguide without informing us of his intention . . . His paper came to hand while this one was in proof and it has been possible to do little more than delete the proposed name and substitute *eisentrauti* for it in the text and table." Colston (1981) reported 11 specimens of *eisentrauti* (6 ♂♂ and 5 ♀♀), and compared them with *M. zenkeri*, which he grouped with *eisentrauti* in a superspecies.

Prigogine (1985) gave the status of *M. eisentrauti* as "species" (Appendix, Table A.1, p. 106), without comment. Although Keith (pers. comm.), Short (pers. comm.) and Traylor (pers. comm.) think that *M. eisentrauti* is a good species and that it forms a superspecies with *M. zenkeri*, it seems to us impossible at present for lack of pertinent biological data to decide whether *M. eisentrauti* is either an allospecies of *M. zenkeri* (Sibley & Monroe 1990: 44), or else a *species inquirenda*. Conservatively, we classify it for now as Ba.

Alaudidae

(7) *Mirafra ashi* Colston 1982, *Bull. Brit. Orn. Cl.* 102(3): 107—13 km north of Uarsciek, southern Somalia, 2°17′N, 45°50′E.
= *Mirafra ashi* (Ab).

This is the fourth new species of larks of the genus *Mirafra* to have been described since 1955, the others being *M. williamsi* MacDonald 1956 (discussed in Mayr 1971), *M. sidamoensis* Erard 1975 and *M. degodiensis* Erard 1976 (discussed in Mayr & Vuilleumier 1983). *M. ashi* is based on a series of 6 specimens "collected by Dr J. S. Ash 13 km north of Uarsciek (=Warsheikh), some 80 km NE of Mogadiscio, in southern Somalia on 9 and 10 July 1981". The type is housed at the BMNH (Tring), No. B.M. 1982-3-1. The new species was compared chiefly with *M. somalica*, which "has been collected at Uarsciek, 2°17′N, 45°44′E" and is thus sympatric with it. Of comparisons with *Mirafra* larks other than *somalica*, Colston (1982: 107) only stated: "Comparison with BMNH material shows the Uarsciek larks to be similar in structure and plumage to other *Mirafra* species and closest to *M. somalica.*" "Whereas *somalica* is bright cinnamon-rufous above, *ashi* is greyish-brown above with a very faint overlaying wash of cinnamon. It is also considerably more streaked and scaly looking above in general appearance than *somalica*" (Colston 1982: 107). A table gave measurements of *M. ashi* and *M. somalica* and showed *ashi* to be smaller. Further brief comparison was made between *M. sharpei, M. ashi*, and *M. somalica: sharpei* has no white in the tail, whereas *M. ashi* has narrow white edges to outer retrices, and *M. somalica* much wider white edges. No illustrations accompanied the original description.

Prigogine (1985, Appendix, Table A.1: 106) accepted *M. ashi* as a species without comments. Keith (pers. comm.) believes that *M. ashi* is a good species but that it is premature to ascribe it to a superspecies until its voice and behaviour are known. Sibley & Monroe (1990: 649) maintain *M. ashi* as a species. Ash (*in litt.* 1 June 1988) wrote that "*Mirafra ashi* [had] been looked for, but not refound". Given the difficulties of species-level systematics in larks of the genus *Mirafra*, one would have wished for more biological information bearing on the status of the new taxon. Pending such evidence, however, we keep *M. ashi* as a species (Ab).

Hirundinidae

(8) *Hirundo perdita* Fry & Smith 1985, *Ibis* 127: 2—Sanganeb Light House, Red Sea (19°43½′N, 37°26′E).
=? *Hirundo perdita* (Ba).

This new species is based on a single specimen found dead on 9 May 1984 by the junior author at the Sanganeb lighthouse, located on a reef "20 km northeast of Port Sudan and 14 km due east of the coast" (Fry & Smith 1985: 1). During a stay at Sanganeb lighthouse for 2 weeks from 30 April 1984 to at least 9 May 1984 many Palaearctic migrants were seen or caught, including a number of swallows: "one House Martin *Delichon urbica*, 2 Red-rumped Swallows *Hirundo daurica*, up to 100 *R. riparia* per hour and up to 500 *H. rustica* per hour" (Fry & Smith 1985: 2). The type (BMNH No. 1984.5.1) consists of wings and tail only. The original description is illustrated by a colour plate, which shows the dead bird (dorsal and ventral views) before it decomposed.

The putative new species was compared to *H. spilodera*, from which it differs in several colour characters, especially steely blue crown, blackish forehead and lores, grey rump, white chin, and bluish-black throat and upper breast. On the basis of these differences in a single unpreserved specimen, Fry & Smith (1985) concluded that "it clearly represents a new form, to which we accord specific rank" (p. 2). The breeding range of the putative new species is unknown.

Sibley & Monroe (1990: 579) included *perdita* as an allospecies of the *Hirundo [spilodera]* superspecies, adding: "May be conspecific with some member of the *H. [spilodera]* superspecies". Keith (pers. comm.) thinks *H. perdita* is a good species but that it is premature to link it with any other species. Parkes (*in litt.*) is sceptical of *H. perdita* being a valid species: "strangely, considering the time and place of discovery, no mention was made of the (to me) strong possibility that it is a hybrid of Palearctic origin". Remsen (*in litt.*) also wondered about *perdita* being a hybrid. In view of the very incomplete nature of the unique type, we agree with Parkes and Remsen that a hybrid origin cannot be ruled out.

Pending further specimens (and the postscripts in Fry & Smith 1985: 6, notwithstanding), we judge it prudent to treat *H. perdita* as a *species inquirenda* (category Ba).

Pycnonotidae

(9) *Phyllastrephus leucolepis* Gatter 1985, *J. f. Ornith.* 126(2): 155—20 km NW Zwedru near Cavalla River, Grand Gedeh County, Liberia (6°12′N, 8°11′W).
=*Phyllastrephus leucolepis* (Ab).

This species is described on the basis of the unique type, a mummified specimen ('Mumienpräparation') that had been damaged by the shot and by ants, and is now housed at the Alexander Koenig Museum, Bonn (No. ZFMK 84.221). The original description was accompanied by a colour plate. The new species was observed several times between October 1981 and January 1984, when the type was collected. Gatter (1985: 160, 161) ruled out conspecificity with the sympatric *Phyllastrephus icterinus* on several grounds, including morphological differences enhancing behavioural characteristics, especially light patches in the wing "used as an optical signal in the dark forest". Keith (pers. comm.) believes that *P. leucolepis* is a good species, quite unlike anything else, and that its nearest relative is hard to guess. Sibley & Monroe (1990: 588) accepted *P. leucolepis* as a full species. In view of the numerous sibling species among bulbuls, we tentatively accept the view that *P. leucolepis* is a distinct new species (Ab), but look forward to more data.

Muscicapidae (Timaliinae)

(10) *Stachyris latistriata* Gonzales & Kennedy 1990, *Wilson Bulletin* 102(3): 368—at an altitude of 1530 m, 11°8′N, 122°14′E, 1.1 km SSW of the peak of Mt. Baloy, Barangay San Augustin, Municipality of Valderrama, Antique Province, Panay, Philippines.
=*Stachyris [striata] latistriata* (Ac).

A babbler of the genus *Stachyris* collected on 6 March 1987 from Mt. Baloy (Panay Island) differed sufficiently from *S. striata* (Luzon) and *S. nigrorum* (Negros) to suggest that it belonged to a new species. Consequently an expedition was launched in 1989 to the same area, and

35 specimens of this very common species were obtained: 18 skins, 13 skins with trunk skeletons, 3 fluid-preserved specimens, and 1 skeleton. Frozen tissues were also collected from 10 specimens. The type is in the National Museum of the Philippines (No. 16663). The paratype series consists of 15 specimens in the NMP and 16 in the Cincinnati Museum of Natural History. The original description includes a colour plate, 2 black and white photographs of the holotype, and an extensive discussion including details on habits and behaviour, habitat (illustrated with 2 black and white photographs), distribution (with a map), breeding (2 photographs of nest and nestlings), and vocalization.

This careful paper leaves no doubt that the new taxon is indeed a distinct new member of the *Stachyris [striata]* superspecies (category Ac). Dickinson *et al.* (1991) also list this taxon as a full species, but without discussing superspecies affinities.

Table 1 in Gonzales & Kennedy (1990: 371) gave a summary of character variation in the 3 taxa of the *Stachyris [striata]* superspecies that are most closely related. *S. latistriata* has a broader black band on the forehead; greenish olive crown, hind neck, mantle, and tail; broad black streaks on breast and flanks; and bluish olive legs and feet. The less closely related *S. hypogrammica* is discussed in the text. (p. 370). Note that *S. nigrorum*, a member of this superspecies, was described as recently as 1952 by Rand & Rabor. In his comment on this taxon, Mayr (1957: 29) had written: "Distantly related to *S. striata* of the mountains of northern Luzon, but fully deserving specific rank". Another member of the *S. [striata]* superspecies, *hypogrammica* was described by Salomonsen (1961). Of that taxon, Mayr (1971) wrote: "This species is clearly related to highland species of the Philippines, *striata* (Luzon) and *nigrorum* (Negros), but is sufficiently different, to judge from the description, not to form a superspecies with them. Six other specimens were collected with the type."

Besides the 3 species of *Stachyris* cited above, 3 other babbler species have been described from the Philippines in recent years: *Napothera rabori* from northern Luzon in 1960, *Micromacronus leytensis* from Leyte in 1962 (both reviewed by Mayr 1971: 305), and *Napothera sorsogonensis* from southern Luzon in 1967 (see Mayr & Vuilleumier 1983: 219). Yet another *Stachyris* species, *rodolphei*, from northwestern Siam [Thailand] was reduced to the status of a subspecies of *Stachyris ruficeps* by Zimmer & Mayr 1943: 257–258. It seems likely that careful explorations of little known areas of Asia, such as those visited by Gonzales & Kennedy in the Philippines, will yield yet other new Timaliinae in the future.

Muscicapidae (Sylviinae)

(11) *Cettia carolinae* Rozendaal 1987, *Zool. Mededel.* 61(14): 179—forest c. 6 km northwest of Bomaki, northwest of Saumlaki across Saumlaki Bay, Yamdena Island (Pulau Yamdena), Tanimbar Islands, South Moluccas, Indonesia, 7°53′S, 131°15′E, altitude 70 m.

= *Cettia carolinae* (Ab)

The type series includes, besides the holotype, 6 other specimens, collected by the author during field work on Yamdena Island between 23

August and 8 November 1985 and are housed at the Rijksmuseum van Natuurlijke Historie, Leiden. The habitat, in primary monsoon forest, and second growth, is illustrated by 3 black and white photographs. One colour photograph and 2 black and white photographs illustrate living birds that were later collected. Because the systematics of warblers of the genus *Cettia* are difficult, the author not only made extensive comparisons of skins of other *Cettia* species [*C. fortipes, C. vulcania, C. (diphone) seebohmi, C. (Psamathia) annae, C. (Vitia) ruficapilla*, and *C. (Vitia) parens*], but also used evidence from vocalizations from several *Cettia* taxa. In plumage characters, especially colour, *Cettia carolinae* resembles southwest Pacific *C. ruficapilla badiceps* and *C. r. castaneoptera* more than closer geographic neighbours like *C. vulcania everetti* from Timor.

On the basis of vocal characters, *C. carolinae* also seems to be more closely related to Pacific taxa of the *C. ruficapilla* group (formerly in the genus *Vitia* but merged in *Cettia* by Orenstein & Pratt 1983). However, vocalizations as depicted in Fig. 12 of Rozendaal's paper seem to ally *carolinae* with *fortipes davidiana*. The description of this undoubted new species is thorough and carefully prepared and Rozendaal has pointed out areas in which further work is necessary before superspecies affiliations can be worked out. A map illustrating the distribution of the various taxa would have helped greatly.

Sibley & Monroe (1990: 609) accepted *C. carolinae* as a full species, and we do so tentatively (Ab). Further data are needed to clarify superspecies limits.

(12) *Cichlornis llaneae* Hadden 1983, *Bull. Brit. Orn. Cl.* 103(1): 23—Crown Prince Range, 5000 ft (1550 m), central Bougainville Island, North Solomons Province, Papua New Guinea, c. 6°19′S, 155°30′E. = *Cichlornis [whitneyi] llaneae* (Ac).

The type specimen of this new thicket warbler was collected by Hadden (1983) on 17 June 1979, and is housed at the AMNH (No. 824713). A nest and egg were also collected, and are at the AMNH. This distinct new taxon of the genus *Cichlornis* is allopatric and different from *C. w. whitneyi* (Espiritu Santo), *C. w. turipavae* (Turipave), and *C. grosvenori* (New Britain). Little is known about these birds, which are represented by very few specimens in museum collections. Diamond (*in litt.*) suggested the possibility that an undiscovered *Cichlornis* exists in the mountains of New Ireland.

Whether *Cichlornis, Ortygocichla, Trichocichla, Buettikoferella* and *Megalurulus* are all congeneric, as proposed by Orenstein (*in* Hadden 1983), remains to be determined, a view shared by Diamond (*in litt.*). Mayr (in Mayr *et al.* 1986: 47) considered *C. whitneyi, llaneae* and *grosvenori* as separate species, not included in a superspecies (see also Ripley 1985). Sibley & Monroe (1990: 625) included these 3 taxa as allo-species of the [*whitneyi*] superspecies, a view with which 2 of us concur (category Ac).

Muscicapidae (Malurinae)

(13) *Malurus campbelli* Schodde & Weatherly, *in* Schodde 1982, *The Fairy Wrens: A Monograph of the Maluridae*, Lansdowne Edition,

Melbourne: 32—Bosavi, Southern Highlands Province, Papua New Guinea, 800 m altitude 6°24′S, 142°50′E.

= *Malurus grayi campbelli* (Bb).

The formal description of *M. campbelli* was published in January 1983 by Schodde & Weatherly in *Emu* 82 (suppl.): 308, [even though volume 82 carries 1982 as year of publication]; but the new taxon was actually confusingly 'described' earlier as an entry by Schodde & Weatherly in Schodde's monograph of the fairy wrens, copyrighted in 1982, as cited above. A colour plate illustrated the putative new taxon, but no type was designated. All this confusion is regrettable. Also regrettable is the fact that the description (whether the one in 1982 in Schodde's book, or the one in 1983 in the Emu supplement) was not based on a museum specimen, but on live birds and photographs. The putative male in a photograph to be distributed to various museums was designated as the type in the 1983 paper. At the time of writing this, no such photograph has been received at the AMNH. Only later were specimens collected and described (Schodde 1984).

Originally, in 1980, 2 birds were caught in mist nests by R. W. Campbell, photographed, and released. In 1981, 3 additional birds were banded and released. Then in 1982, 5 birds (2 ♂♂, 1 ♀, 2 fledglings) were collected by R. W. Campbell and R. D. Mackay at the type locality. Four of these birds are housed at the Papua New Guinea Museum and Art Gallery, Port Moresby, and one (subadult male) is on permanent loan at the Australian National Wildlife Collection, CSIRO, Canberra (No. 26467). To compound the problems created earlier, and as Schodde (1984: 249) wrote: "Regrettably, none of the adults can be identified as a syntype (or selected as a lectotype) because none is from the banded birds on which the original description was based. That description first appeared in 'The Fairy Wrens: A Monograph of the Maluridae' (Schodde 1982), and takes its date from the issuing of the first numbers of that work in August 1982".

Originally, *M. campbelli* was thought by Schodde & Weatherly (1982, 1983) to be closely related to the allopatric *M. grayi*, "with which it forms a superspecies" (Schodde & Weatherly 1983: 308), differing from it in several colour characters and in its smaller size. In the 1984 paper, however, Schodde (1984: 250) thought that *M. campbelli* also "seems to have links as close to Wallace's Wren *Sipodotus wallacii* as to any other member of *Malurus*; and the corollary, that *Sipodotus* is closer to *M. campbelli-grayi* than to any other group in *Malurus*, seems even clearer".

Sibley & Monroe (1990: 424) included *M. grayi* and *M. campbelli* in the *M. [grayi]* superspecies. Mayr (in Mayr *et al.* 1986: 393) considered *campbelli* as a subspecies of *grayi*. Recently, LeCroy and Diamond (ms) have been able to compare 32 of the 37 known specimens of *Malurus grayi* and *M. campbelli*. Their as yet unpublished study allowed them to recognize "the previously unappreciated geographic and individual variation in *M. grayi*, as well as to confirm the reality of certain previously reported sex-related differences that had been questioned". Beehler *et al.* (1986) regarded *campbelli* as a race of *M. grayi* in their recently published field guide to New Guinea birds on the basis of this analysis. We follow the same treatment here (Bb).

(14) *Gerygone ruficauda* Ford & Johnstone 1983, *Western Austr. Nat.* 15: 133—"Thirteen Mile River", Rockingham Bay, Queensland.
= *Gerygone chrysogaster* (Bc).

This new species of *Gerygone* was based on 3 specimens, 2 in the Australian Museum, Sydney (the type is number 0.17290) and one in the AMNH. It was said to be closest to *G. magnirostris* and *G. chrysogaster*. Schodde (1985) reduced *G. ruficauda* to the synonomy of *G. chrysogaster*, a view accepted by Sibley & Monroe (1990: 443). Some ornithologists (e.g. Boles, *in litt.*) even doubt that the specimens can be identified. We place it in category Bc (synonyms).

Incredibly, in this day and age, and given the profound experience of the late senior author in systematic and evolutionary biology, this putative new species in a difficult Australasian genus was described on the basis of 3 old and uncertainly labelled specimens. The wording smacks of an earlier era in ornithology, now past and gone: "Though there is some doubt regarding the exact collecting localities of these specimens, they are so distinct and yet uniform in morphology, a description of a new taxon is warranted" (Ford & Johnstone 1983: 133).

Muscicapidae (Platysteirinae)

(15) *Batis occultus* Lawson 1984, *Bull. Brit. Orn. Cl.* 104(4): 145—Grassfield, Mt. Nimba, Liberia (7°30′N, 8°35′W), altitude 550 m.
= *Batis poensis occulta* (Bb).

This is the second new species to be described from Mt. Nimba in the 1981–1990 period (see *Melignomon eisentrauti* earlier). *Batis occultus* was described on the basis of 13 specimens (?including the type) from Ivory Coast, Cameroon, Nigeria, Ghana and Liberia. The type, from Liberia, is housed at the BMNH, number 1977.20.2078. Mainland *B. occultus* differs from the insular populations (*B. poensis*) from Fernando Pó in colour and size. Mainland *occultus* is slightly smaller than insular *poensis* and has a conspicuous white supercilium that is lacking in *poensis*.

Lawson (1984: 145) said "It is here contended that the colouration differences between them [insular and mainland populations] are sufficiently marked for them to be considered distinct species". Keith (pers. comm.) thinks that *B. occultus* forms a superspecies with *B. poensis*. Sibley & Monroe (1990: 503) treated *occultus, poensis* and *minulla* as allospecies of the *B. [minulla]* superspecies. Traylor (*in litt.*) "finds this [taxon] hard to accept as a species", and "would accept *occultus* as a subspecies of *poensis*, but not as a species unless fresh Cameroon material shows all the differences". We agree with Traylor that *occultus* is best considered a subspecies of *poensis* (Bb).

Note that, following Clancey (1989) *occultus* should be spelled *occulta*.

Nectariniidae

(16) *Nectarinia rufipennis* Jensen 1983, *Ibis* 125(4): 447—Mwanihana Forest Reserve, Uzungwa Mountains, above the village Sanje,

Kilombero District, Morogoro Region, eastern Tanzania. Altitude 1000 m.
=*Nectarinia rufipennis* (Ab).

This new sunbird was described on the basis of a male (holotype, in the Zoological Museum, Copenhagen, No. 8.12.1981.1) and a female (in the BMNH, No. 1981.9.7) collected in 1981 in a remote area of rainforest in eastern Tanzania. The new birds (illustrated in a colour plate) were compared to a variety of African sunbirds of the genus *Nectarinia*, including the *N. chalybea* species-group, the *N. afra* superspecies, and the *N. regia* superspecies. "The most remarkable [differences shown by *N. rufipennis*] are the bronzy throat patch of the male and the rufous edges of the flight feathers of both sexes, characters which appear unique among African sunbirds" (Jensen 1983: 449). In another, popular, article, Jensen (1985) published a colour photograph of a female, gave details about the original discovery of this new species, and indicated that during a subsequent expedition, he found that the new species was abundant from c. 4000–6000 feet, in montane forest habitat with lichens and mosses and epiphytic plants growing on trees. The area of this habitat in Mwanihana Forest "encompasses perhaps 20 square miles" (Jensen 1985: 21).

Sibley & Monroe (1990: 666) wrote: "Relationships unclear; a unique species with no certain affinities". Keith (pers. comm.) believes that *N. rufipennis* is very distinctive and not clearly allied to any other sunbird species. We agree that this new sunbird is a valid species with no clear affinity to members of an existing superspecies (category Ab).

Meliphagidae

(17) *Meliphaga hindwoodi* Longmore & Boles 1983, *Emu* 83(2): 59—Massey Creek, Clarke Range, Queensland (21°04′S, 148°35′E).
=*Meliphaga [frenata] hindwoodi* (Ac).

This new species of honeyeater is described on the basis of 25 specimens, deposited at the Australian Museum and the Queensland Museum. The holotype is No. 0.17574 in the Queensland Museum. *M. hindwoodi* appears to be restricted to the Clarke Range, 80 km west of Mackay, Queensland. It differs from allopatric *M. frenata*, which occurs on the Atherton Tableland (Australia), and from *M. subfrenata* (New Guinea highlands), in having more grey in its plumage and streaked underparts. Comparisons of similarities and differences between *M. hindwoodi* and its relatives *frenata* and *subfrenata*, as well as *chrysops* and *obscura*, are carefully made and illustrated by photographs, drawings and tables. Longmore & Boles (1983) proposed a reconstruction of vegetational sequences in Australia and New Guinea to help explain the evolution of taxa in the *M. frenata* species-group.

Sibley & Monroe (1990: 431) accepted *hindwoodi* as an allospecies of the *Lichenostomus [frenatus]* superspecies. For an explanation of their use of the generic name *Meliphaga* instead of *Lichenostomus*, see Longmore & Boles (1983: 60). We believe *hindwoodi* to be an allospecies of *frenata* (category Ac), and we agree that the *Meliphaga-Lichenostomus* complex needs more study.

Ploceidae (Ploceinae)

(18) *Ploceus burnieri* Baker & Baker 1990, *Bull. Brit. Orn. Cl.* 110(1): 52—Ifakara 08°08′S, 36°40′E, in Morogoro Region, east central Tanzania, on the northern bank of the Kilombero River, 320 km southwest of Dar es Salaam, altitude 250 m.

= *Ploceus burnieri* (Ab).

This new weaver was described on the basis of 4 specimens (2 ♂♂ and 2 ♀♀). The ♂ 'holotype' (= syntype) is deposited at the BMNH, No. 1989-7-1, as is the ♀ 'holotype' (= syntype) No. 1989-7-2. The 2 paratypes are deposited at the University of Dar es Salaam Museum of Biology. The original description includes a colour plate painted from the ♂ and ♀ syntypes and photographs of live birds. The new weaver was observed breeding in riverside swamps containing *Phragmites*. A nest was collected and deposited at the BMNH. The authors compared *P. burnieri* with 57 other taxa of *Ploceus*, especially *P. taeniopterus*, *P. castanops* and *P. subaureus*. Baker & Baker (1990: 58) concluded: "We hesitate to attempt a systematic position for this species. It may well prove intermediate between the 'Masked Weavers' and *P. castanops*, although clearly the nest is closer to that of *P. subaureus*." In spite of the careful description of the new species, and of the extensive comparisons, it is difficult to evaluate the biological validity of this putative new *Ploceus*. The possibility of a hybrid population is discounted: "The large sample size of *P. burnieri* and its isolation from similar species does not suggest a hybrid population" (Baker & Baker 1990: 56). The "large sample size" consists, in fact, of only 4 specimens, and some birds handled live: hardly enough data to interpret potential variability of hybrids. In view of the great difficulties posed by the systematics of *Ploceus* species, we keep *P. burnieri* as a distinct species, (Ab), but stress that only further series of specimens and more extensive biological data will resolve its status.

(19) *Ploceus victoriae* Ash 1986, *Ibis* 128: 331—Entebbe, Uganda, 0°04′N, 32°28′E, altitude 1200 m.

= ? *Ploceus victoriae* (Ba).

This new *Ploceus* weaver was described on the basis of the unique holotype, a male collected 20 March 1983 and deposited at the BMNH, (No. 1985.1.29). The female is still unknown. "Although the specimen is unique, other individuals are known to exist in the field, and it is desirable to describe this as a new taxon at full specific level" (Ash 1986: 331). This species is somewhat similarly marked (facial pattern) as *Ploceus taeniopterus*, *P. melanocephalus*, *P. castanops* and *P. velatus* (diagrammatically illustrated), but seems to have a different wing formula. Furthermore, "*P. victoriae* differs markedly from *taeniopterus* in being a non-colonial and solitary species" (Ash 1986: 335). Ash (1986: 336) believed that morphological characters and nesting behaviour differences justify separating this specimen as a full species, and stated that it "can be regarded as a member of a superspecies including *melanocephalus*, *taeniopterus*, *jacksoni*, *dicrocephalus* and *intermedius*". He discarded the possibility of hybridization, chiefly on the ground that: "The probability of seeing several hybrids looking alike in the same area in the course of one year seems to be highly unlikely, and would appear to indicate that *victoriae* is not a hybrid. Also, at no time were any mixed pairs seen in the colonies of breeding Ploceids, which often contained several species'' (Ash 1986: 335).

Louette (1987) has questioned the specific status of *victoriae*, in a critique of Ash's (1986) description, in which he pointed out that this specimen could be the result of several hybrid combinations (*P. castanops* × *P. melanocephalus fischeri* or *P. castanops* × *P. jacksoni*). Louette (1987: 405) also points out that several *Ploceus* species breeding at Entebbe have been found breeding in colonies, ''but sometimes solitarily or a couple together''. Thus the solitary nesting behaviour of *P. victoriae*, based on limited field evidence, might not be as significant as Ash (1986) suggested (see also Ash 1987 in reply to Louette 1987).

Although Sibley & Monroe (1990: 683) included *victoriae* in the *Ploceus [taeniopterus]* superspecies, they also stated that *victoriae* is ''possibly a subspecies of *P. taeniopterus* or some other species of 'masked weaver' ''. At the end of his paper, Ash (1986: 336) wrote that ''without more study and more specimens of *victoriae* [its status] is largely conjecture''. Indeed, we feel that there is too little evidence in this case, and for the moment maintain *P. victoriae* as a *species inquirenda* (category Ba).

(20) *Ploceus ruweti* Louette & Benson 1982, *Bull. Brit. Orn. Cl.* 102(1): 26—Kinsamba, near the eastern edge of the maximum level of Lake Lufira (i.e. Lake Shangalele, or Tshangalele—cf. *Times Atlas*, 1975: 203, at 10°50′S, 27°03′E, and map in Ruwet 1963: facing 60), Zaïre.
= *Ploceus [reichardi] ruweti* (Ac).

The unique holotype, ''a male in almost complete breeding dress'', was probably collected in March 1960, and is now kept in the KMMA (No. 113379). This specimen ''has been compared by both of us with every conceivable form of *Ploceus* (males in breeding dress), both in the KMMA and in the British Museum (Natural History)'' (Louette & Benson 1982: 25–26). The specimen is illustrated, together with a male of *P. reichardi*, in a black and white photograph. Other photographs in the original description include a nest attributed to *P. ruweti*, a colony of nests attributed to *P. ruweti*, and the typical habitat (swamp) of *P. ruweti* in the Lufira delta. Louette & Benson (1982) make a good case to suggest that *P. ruweti* is a member of the *reichardi* group, including also *P. reichardi* and *P. katangae* (with *upembae* as a subspecies). This group of swamp-dwelling allopatric forms, seem to form a superspecies. Sibley & Monroe (1990: 683) treated these 3 forms as members of the *P. [reichardi]* superspecies. Traylor (*in litt.*) ''would have to accept the conclusions'' of Louette & Benson (1982). We feel that this treatment seems reasonable (hence our classification as Ac), but given the incomplete information available to date on these birds, we emphasize that the possibility that *P. ruweti* is a subspecies of *reichardi* has not been sufficiently addressed.

Ploceidae (Viduinae)

(21) *Vidua raricola* Payne 1982, *Misc. Publ. Mus. Zool., Univ. Michigan*, No. 162: 16—Banyo, Cameroon, 6°45′N, 11°50′E, altitude 1050 m.
= *Vidua raricola* (Ab).

The holotype, a male in breeding plumage, housed at the University of Michigan Museum of Zoology (number 204008), was collected by Payne on 6 November 1980. Other material used to describe *V. raricola* include 17 specimens from Cameroon, one from Sierra Leone, and 2 from Ghana. "The species name *raricola* refers to the affinity of this brood parasite species for its foster species and song model, the Black-bellied Firefinch *Lagonosticta rara*" (Payne 1982: 33). *V. raricola* differs from other indigobirds *Vidua* "by the mouth pattern of the immature birds, which mimic the mouth pattern of nestling Black-bellied Firefinches *Lagonosticta rara*" (Payne 1982: 17). Males mimic the songs of *L. rara*. It seems impossible to identify some individual specimens of *Vidua* unless their host species is known. Also, variability of plumage colour in *V. raricola* matches that of other *Vidua* species. This clearly presents exceptional difficulties for systematics. But, as Payne (1982: 17–18) stated: "the morphogenetic uniqueness of certain young indigobirds in mimicking the mouth pattern of *L. rara*, the restriction of these young to the localities where *L. rara* occur and where adult male indigobirds mimic the songs of *L. rara*, and the morphogenetic distinctiveness of these males from other locally sympatric male indigobirds that mimic other species of firefinches in Cameroon and in Sierra Leone together indicate that the population [*raricola*] behaves as a species distinct from the others". As Payne (1982: 18, 22) himself pointed out: "This diagnosis recognizes that it may be impossible to identify to species those birds in regions where the song behaviour is unknown." Female and juvenile *V. raricola* are indistinguishable from similar plumages of other species of indigo birds.

In Cameroon, Payne (1982) found 3 sympatric species of *Vidua*, *V. raricola* mimicking *Lagonosticta rara*, *V. funerea* mimicking *L. rubricata*, and *V. wilsoni* mimicking *L. rufopicta*. "No habitat differences were apparent between the green *V. raricola* and blue *V. funerea* at Banyo; the birds were on neighbouring territories in scrub at the edge of fields cultivated for manioc and pineapple" (Payne 1982: 26).

V. raricola occurs together with its host species *Lagonosticta rara* from Sierra Leone to Ghana, Nigeria and Cameroon, and probably also in parts of Zaïre and of Sudan.

Sibley & Monroe (1990: 700) accepted *V. raricola* as a full species. Traylor (*in litt.*), who has studied indigobirds, made the point that *V. raricola* (and the next species *V. larvaticola*) must be considered good species "if you accept Payne's thesis that the species of *Vidua* are each obligate nest parasites on a single species of *Lagonosticta, and* that they can be identified by mimicking the songs of their respective hosts, *and* by the juvenals having the same palatal markings" (italics ours). We classify *raricola* as Ab, a species not clearly a member of a superspecies.

(22) *Vidua larvaticola* Payne 1982, *Misc. Publ. Mus. Zool., Univ. Michigan*, No. 162: 33—Zaria, Nigeria, 11°10′N, 7°40′E.
= *Vidua larvaticola* (Ab).

The holotype, a male in breeding plumage, kept in the University of Michigan Museum of Zoology (number 216994), was collected by Payne on 6 August 1968. Additional specimens used to describe *V. larvaticola* include 21 birds from Nigeria. "The species name *larvaticola* describes the affinity of this indigobird for its host species *Lagonosticta larvata*" (Payne 1982: 41).

"The species *V. larvaticola* is characterized by its species-specific mimicry of the Black-faced Firefinch *Lagonosticta larvata*" (Payne 1982: 34). As in *V. raricola*, it is impossible to identify some specimens of *V. larvaticola*, especially females and juveniles, but males also, unless they were collected with their host species (males vary regionally from green to blue in colour). Immature *V. larvaticola* have mouth markings that mimic those of *L. larvata*. Further, male *V. larvaticola* mimic the vocalizations of *L. larvata*.

Payne (1982: 36–39) found local sympatry in Nigeria between *Vidua chalybeata* (and its host *Lagonosticta senegala*), *V. larvaticola* (and host *L. larvata*), and *V. wilsoni* (and host *L. rufopicta*). *V. larvaticola* occurs in Nigeria and Cameroon, and probably also locally in other west African countries (The Gambia, Guinea-Bissau, Guinea, Mali, Ivory Coast, Ghana, Togo), as well as in Sudan and elsewhere in central Africa. Payne's (1982) Fig. 21 illustrates the distribution of *V. larvaticola* and its host *Lagonosticta larvata*.

As for *Vidua raricola*, Payne's (1982) evidence strongly suggests specific distinctness of *V. larvaticola*, a view adopted by Sibley & Monroe (1990: 700). Although more work is needed to establish clearly the status of *V. raricola*, we classify it as Ab.

NEW WORLD

Anatidae

(23) *Tachyeres leucocephalus* Humphrey & Thompson 1981, *Occ. Papers Mus. Nat. Hist. Univ. Kansas*, No. 95: 3—Puerto Melo, Provincia de Chubut, Argentina (45°01′S, 65°50′W).

= *Tachyeres [pteneres] leucocephalus* (Ac).

The holotype, an adult male, no. 52694 in the Museo Argentino de Ciencias Naturales (MACN), Buenos Aires, Argentina, was collected on 24 September 1979 by Humphrey & Thompson (1981). The description is based on material deposited at the MACN (one skin and partial skeleton, the holotype); Southwestern College, Winfield, Kansas (6 skins and partial skeletons); and Museum of Natural History of the University of Kansas, Lawrence (25 complete skeletons). *T. leucocephalus* is 'abundant' at the type locality, Puerto Melo, "and presumably other localities with rocky shorelines along the coast of Chubut" (Humphrey & Thompson 1981: 8); elsewhere in the paper, the authors mention the species having been photographed at Punta Tombo and Camarones, and state that *T. leucocephalus* "probably occurs in appropriate habitat along the coast of Chubut from Bahía Bustamante north perhaps as far as Puerto Madryn and Península Valdez" (p. 7). See Beno (1982) for a popular account of the discovery of this species.

"*Tachyeres leucocephalus* is distinct from all known species in the genus [*pteneres, brachypterus* and *patachonicus*] in terms of various combinations of characters, including body weight, proportions of certain measurements, shape of humerus and posterior region of sternum, and colouration of the feathering of the head and neck in various plumages" (Humphrey & Thompson 1981: 5). A colour plate illustrates head plumages of males and females, in various moult stages, and of a juvenal.

On the basis of a phylogenetic study, Livezey (1986) concluded that the 3 flightless taxa of *Tachyeres* were a monophyletic assemblage, within which *T. leucocephalus* and *T. brachypterus* (Falklands) were the most closely related taxa (sister species). Livezey (1986) proposed a model of differentiation, according to which allopatric speciation between proto-*leucocephalus* and proto-*brachypterus* was the latest of several postulated vicariance events. In another study, Corbin *et al.* (1988) analyzed steamer-ducks by means of electrophoretic characters, and confirmed the close relationships of the 3 flightless taxa, and the sister-species relationship of *brachypterus* and *leucocephalus*. Corbin *et al.* (1988: 779) speculated that "the divergence of lineages leading to *T. brachypterus* and *T. leucocephalus* would have occurred about 13,000 years ago".

Sibley & Monroe (1990: 32) placed the 3 flightless taxa of *Tachyeres* in a single superspecies. Humphrey (*in litt.*) felt that they are too different to be included in a superspecies. One of us (F V) recently saw *T. leucocephalus* at the type locality and Cabo dos Bahias, and feels that still more study is needed to clarify relationships between it and *T. pteneres*. Given the taxonomic problems posed by the different populations of *Tachyeres*, we tentatively place the 3 flightless steamer ducks in a single superspecies *T. [pteneres]*, and hence classify *T. leucocephalus* as Ac.

Psittacidae

(24) *Pyrrhura orcesi* Ridgely & Robbins 1988, *Wilson Bulletin* 100(2): 174—c. 9.5 road km west of Piñas, altitude c. 900 m, 3°40′S, 79°44′W, Prov. El Oro, Ecuador.

= *Pyrrhura [melanura] orcesi* (Ac).

The holotype, an adult male, is deposited in the Academy of Natural Sciences of Philadelphia (ANSP) (No. 177523). Sixteen additional specimens exist, 14 at the ANSP, one in the BMNH, and one in the Museo Ecuatoriano de Ciencias Naturales in Quito. The 17 specimens come from 2 localities, in Provinces El Oro and Azuay. *P. orcesi* (illustrated by a colour plate in the original description) is allopatric with various populations of *P. melanura*, from which it differs in having a red forehead, obsolete scaling on the breast, and greener crown (variation illustrated in a colour plate including both species and their geographic distribution). *P. orcesi* appears restricted geographically and occurs in humid mid-montane forest between 600 and 1100 m. (except that the BMNH specimen was collected at 300 m).

Forshaw (1989: 493) treated *orcesi* as a full species. Sibley & Monroe (1990: 126) treated it as a member of the *P. [melanura]* superspecies, and we treat it likewise here (Ac).

(25) *Amazona kawalli* Grantsau & Camargo 1989, *Rev. Brasil. Biol.* 49(4): 1018— Rio Juruá, Amazonas, Brazil (region circumscribed in

a radius of c. 75 km from Seringal de Mato Piri, along the right bank of the Rio Juruá, downstream from the town of Eirunepé, on the left bank of the Rio Juruá [6°38′S, 69°50′W]).
= ? *Amazona kawalli* (Ba).

The description of this new species is based on 3 birds, the holotype (a female, housed in the Museum of Zoology of the University of São Paulo (MZUSP), number 2727) collected in 1902, and 2 paratypes (one, female, in MZUSP, number 3478, also collected in 1902; the second, a male, in the collection of Rolf Grantsau, number 7577, from Santarém, Pará, collected in 1970). This new taxon has previously been confused with *A. farinosa*. It differs from *farinosa* in bill colour, a white patch of skin at the base of the bill, an ashy grey ocular ring, pale green carpal joint without any trace of red, generally green colour, external rectrices with red at the base of the inner vane, restricted amount of pale green at distal tip of central rectrices. Two live birds are also cited by Grantsau & Camargo (1989), in Nelson Kawall's collection. The new bird was compared to a series of 25 *Amazona f. farinosa*. A colour plate accompanies the original description.

Grantsau & Camargo (1990) essentially re-published their 1989 description in the semi-popular German journal *Trochilus*, with the same colour plate (but less well-produced), but with the addition of a table of measurements of *A. kawalli* and *A. f. farinosa*, and a map of the distribution of *A. kawalli*, showing the 2 localities, 1700 km apart.

We feel that there is not enough evidence at present to decide what the status of this form is, hence our classification as Ba.

Strigidae

(26) *Otus marshalli* Weske & Terborgh 1981, *Auk* 98(1): 1—Cordillera Vilcabamba, 12°38′S, 73°36′W, altitude 2180 m., Provincia de la Convención, Departamento de Cuzco, Perú.
= *Otus marshalli* (Ab).

The holotype is an adult male kept at the AMNH (number 824160). Eight specimens were available for the original description, all collected from c. 1920–2240 m in the northern Cordillera Vilcabamba, Cuzco, Perú. Since the original description, the species has been found farther north, in the Cordillera Yanachaga (Schulenberg *et al.* 1984). In the Cordillera Vilcabamba, this owl seems to be common and reached its peak abundance between 2130 and 2190 m, where it was "the 29th most commonly netted bird species among a total of 53" (Weske & Terborgh 1981: 4). Its habitat is cloud forest with a luxuriant understorey, including a profusion of clinging bamboo. The new owl differs from other Neotropical owls, except the Central American species *O. barbarus* and *O. clarkii*, in the barred and streaked underparts. No Andean taxon appears to be closely related to *O. marshalli*. The morphological differences between *O. marshalli, O. barbarus* and *O. clarkii* are rather well marked. It is thus unclear whether *O. marshalli* should be included in a superspecies with *barbarus* and *clarkii*.

Further problems are raised by the description of *O. petersoni* (see below, under 27), which Fitzpatrick & O'Neill (1986) compared with *marshalli* and other *Otus* spp. (especially *ingens*, *colombianus* and *watsonii*). These 4 species appear to form a species-group of brown-eyed *Otus*. Note that Fitzpatrick & O'Neill (1986) did not discuss the affinities of *O. clarkii* and *O. barbarus*.

Marshall & King (1988: 335) treated *O. marshalli* as a full species; Sibley & Monroe (1990: 173) included *marshalli* and *petersoni* in a superspecies, an action that may be premature. That *O. marshalli* is a valid species is not in question, but whether it belongs to a superspecies and with what other species is as yet uncertain. Thus our tentative classification of this bird as Ab. It is unfortunate that the voice of *O. marshalli* is unknown.

(27) *Otus hoyi* König & Straneck 1989, *Stuttgarter Beitr. Naturk.*, Ser. A (Biol.), No. 428: 4—La Cornisa, c. 40 km north of the town of Salta, Argentina.

= *Otus atricapillus hoyi* (Bb).

The type, a bird collected by G. Hoy in 1987, is in the ornithological collection of the Staatliches Museum für Naturkunde in Stuttgart (number SMNS 62849); one paratype is in the Museo Argentino de Ciencias Naturales in Buenos Aires, and 8 others in the Instituto Miguel Lillo in Tucumán. These 10 birds differ from *O. choliba* and *O. guatemalae* in several characters (illustrations of skins and sonagrams of vocalizations are provided in the description), and in colour and pattern resemble more closely Central American *O. barbarus, O. marshalli* from Perú (see number 26 above), or else an *Otus* from southern Brazil. The vocalizations of *Otus guatemalae* from Perú appear closer to those of *O. hoyi* than those of other *Otus* spp. *O. hoyi* lives in wet montane forest between c. 1000 and 2600 m, in areas with dense undergrowth. König & Straneck (1989) mentioned the similarity in habitats between *O. hoyi* and *O. marshalli*.

In a later paper, König (1991) examined in detail the relationships of *O. atricapillus, O. sanctaecatarinae* (parapatric) and *O. hoyi* (allopatric), especially through comparisons of vocalization. Together with *O. guatemalae*, König (1991: 213) placed these 3 forms in the *O. [atricapillus]* superspecies. On the basis of this additional evidence, one could either accept his classification or consider *hoyi* as a subspecies of *atricapillus*. For the present we favour the latter designation (Bb).

(28) *Otus petersoni* Fitzpatrick & O'Neill 1986, *Wilson bulletin* 98(1): 2—Cordillera del Cóndor, above San José de Lourdes, Dept. Cajamarca, Perú, 5°02′S, 78°51′W, altitude 1950 m.

= *Otus colombianus petersoni* (Bb).

The holotype is an adult male housed at the AMNH (No. 824049). Nine additional specimens are paratypes. The new species occurs at 4 localities, 2 in southern Ecuador and 2 in northern Perú. An additional (11th) specimen is a Bogotá trade skin (at the Academy of Natural Sciences of Philadelphia). A colour plate accompanies the original description.

The new species lives in subtropical forest, and is sympatric at 3 of the 4 localities with *O. ingens*. After a detailed analysis of morphology and vocalizations, Fitzpatrick & O'Neill (1986) concluded, convincingly, that *O. petersoni* is the sister-taxon of *O. colombianus*, from the eastern Andes of Colombia and Ecuador. "In plumage pattern and colour, *colombianus* and *petersoni* are so nearly alike as to suggest they could be conspecific" (Fitzpatrick & O'Neill 1986: 9). They prefer to treat them as distinct species, but they "emphasize that based upon present data the question cannot be settled unequivocally". Sibley & Monroe (1990: 173) treated *petersoni* and *marshalli* as members of a superspecies. Marshall & King (1988: 335) treated *petersoni* as a subspecies of *colombianus*, and we are inclined to agree with this placement (Bb).

Furnariidae

(29) *Asthenes luizae* Vielliard 1990, *Ararajuba* 1: 121—c. 1100 m. altitude, serra do Cipó, município de Jaboticatubas, Minas Gerais, Brazil.
= ? *Asthenes luizae* (Ba).

This new *Asthenes* was described on the basis of 2 specimens. The holotype, an adult male, "will be deposited at the MZUSP when the work in progress is completed" (Vielliard 1990: 121). At present the holotype is in F. Lencioni's collection (number 349). The paratype, an immature male, is also in F. Lencioni's collection (number 568). Thus, the accessibility of the type specimen is in doubt, and we strongly deplore the practice of having specimens of (putative) new taxa in private collections, as both appear to be in this instance. These birds were collected in December 1985 and December 1988 in the Serra do Cipó, Minas Gerais. A coloured plate of the new bird has been prepared by F. Lencioni (but has not been published—F. Lencioni *in litt.*). A subsequent paper is promised.

The original description only states that F. Lencioni recognized that the specimen he collected in 1985 "belonged to the genus *Asthenes* and that it was a new species" (Vielliard 1990). Nowhere in the original description did the author state whether comparisons had been made between the 2 type specimens and any other Furnariidae, including *Asthenes*. It is thus impossible to make any statement about *Asthenes luizae* on the basis of Vielliard's (1990) description.

More or less simultaneously, Pearman (1990) published a paper on an "undescribed Canastero *Asthenes* species from Brazil". Pearman (1990) apparently published his paper, which seems to deal with the same taxon as Vielliard's (1990) new species, because: "After carrying out extensive fieldwork personally in 1988 and 1989, and due to the long time lapse since the original discovery [in 1985], lack of any information on the species in the literature and no definite forthcoming description, I feel there is a need to publish the present findings" (Pearman 1990: 146). Pearman's (1990) description of the new *Asthenes* species is based entirely on field observations, since "the collecting of specimens was not possible". Pearman (1990), like Vielliard (1990) gave no information concerning the reasons why the 'new bird' belongs in the genus *Asthenes*. Vocalizations (sonagrams) of the 'new species' are compared to those of several species of *Asthenes*. Clearly, the description of a putative new *Asthenes* in Minas Gerais, many km away from the Andean-Chacoan-Patagonian region, where *Asthenes* is distributed, requires substantiation. If correct, such a discovery would be quite interesting biogeographically, and would parallel somewhat the case of *Schizoeaca*, another Furnariidae. For the present, however, this is conjectural. There is simply not enough evidence and the new name must remain, for the time being, a *species inquirenda* (Ba). The practice of naming putative new species the way *Asthenes luizae* was described is not very professional.

(30) *Philydor novaesi* Teixeira & Gonzaga 1983a, *Bol. Mus. Paraense Emilio Goeldi, Nova Série Zoologia*, No. 124: 4—'Serra Branca', Município de Murici (c. 9°15′S, 35°50′W), Alagoas, Brazil, c. 550 m. altitude.
=? *Philydor novaesi* (Ba).

Both the holotype (adult male, number 32029) and the paratype (adult male, number 32028) are housed in the Museu Nacional in Rio de Janeiro (MNRJ). They were collected almost simultaneously in mist nets as part of a mixed flock in a tract of rainforest of northeastern Brazil visited during an expedition in February 1979. These specimens were compared with series of *Philydor atricapillus*, the type of *Philydor hyperythrus*, and colour photos of *P. hylobius* (but about the status of *P. hylobius* see Appendix IV). A black and white drawing (Teixeira & Gonzaga 1983a: 8) illustrated the head pattern of the 4 taxa of *Philydor*. *P. novaesi* differs from *P. atricapillus* in having a narrower and less conspicuous superciliary stripe, and a less well marked postocular band. The mystacal stripe of *P. novaesi* is also less well marked than the one in *P. atricapillus*. The rufous nape band, conspicuous in *P. atricapillus* is lacking in *P. novaesi*. *P. novaesi* is larger and heavier than *P. atricapillus*.

Philydor novaesi and *P. atricapillus* are allopatric (map in Teixeira & Gonzaga 1983a: 13). The authors suggested that the differences between *P. novaesi* and *P. atricapillus* are sufficient to justify their classification as members of a superspecies.

Since the original description, Teixeria *et al.* (1987) have reported 4 additional specimens, including 3 females. "According to this material, the females of *P. novaesi* are identical to males in plumage, and also show no trace of the bright nuchal collar which is very conspicuous in the closely related Black-capped Foliage gleaner *Philydor atricapillus*" (Teixeira *et al.* 1987: 155).

Sibley & Monroe (1990: 408) placed these 2 taxa in the *Philydor [atricapillus]* superspecies. Ridgely (*in litt.*) believed *P. novaesi* to be a good species; Sick (*in litt.*) thought that *P. novaesi* was either an "allospecies or geographic race of *P. atricapillus*"; Fitzpatrick (*in litt.*), however, queried the validity of *P. novaesi*.

In view of the fact that '*Philydor hylobius*' was recently shown by Dickerman *et al.* (1986) to be a synonym of *Automolus roraimae*, we believe that the identification of the correct status of *P. novaesi* must await further, broader comparisons, including other genera of Furnariidae. We classify it for the time being as a *species inquirenda* (Ba).

Formicariidae

(31) *Clytoctantes atrogularis* Lanyon, Stotz, & Willard 1990, *Wilson Bulletin* 102(4): 571—Cachoeira Nazaré, west bank of Rio Jiparaná, Rondônia, Brazil, 9°44′S, 61°53′W, altitude 100 m.
= *Clytoctantes [alixii] atrogularis* (Ac).

The unique type, a female, was mist-netted during an expedition to Rondônia. It is housed at the MZUSP (number 66111); colour slides are on file at the Field Museum of Natural History (FMNH), Chicago, and with VIREO at the Academy of Natural Sciences in Philadelphia. Although 2 males were observed, "subsequent attempts to collect more specimens and observe it further were unsuccessful" (Lanyon *et al.* 1990: 571). The authors point out that they "are reluctant to describe a new taxon on the basis of a single specimen", but that "the bird's features are so distinctive . . . that [they] believe it represents an undescribed species" (Lanyon *et al.* 1990: 571). A colour plate accompanied the original description.

"Within the Formicariidae, only *Clytoctantes* and *Neoctantes* share the unusual bill shape of the new taxon, in which the upper mandibular tomia curve dorsally" (Lanyon *et al.* 1990: 573). *C. atrogularis* differs from females of *C. alixii* chiefly in having a black bib, which is lacking in *C. alixii*. An all black-plumaged male appeared, in the field, different from the grey and black-bibbed male of *C. alixii*. Lanyon *et al.* (1990: 578) remarked: "Five experienced observers spent 1400 field hours at the type locality and accumulated 1450 net-days. The single netted individual and 2 sight records suggest that either: (1) this species is extremely uncommon or secretive, or (2) we encountered only dispersing individuals and that it normally occurs in a different habitat." Actually, both possibilities are likely; many tropical lowland forest avian species in Amazonia are rare. On the basis of the unique type and 2 field sightings, Lanyon *et al.* (1990) concluded that *C. atrogularis* is, indeed, a valid species and not an aberrant *C. alixii*. It seems likely to us that *C. atrogularis* is a valid new species level taxon, forming a superspecies with distantly allopatric *C. alixii* (Ac), but much more evidence is needed.

(32) *Herpsilochmus parkeri* Davis & O'Neill 1986, *Wilson Bulletin* 98(3): 338—c. 15 km by trail northeast of Jirillo on the trail to Balsapuerto, 06°03′S, 76°44′W, altitude 1350 m, Department of San Martín, Perú.
= *Herpsilochmus pileatus parkeri* (Bb).

The holotype is an adult male deposited in the Louisiana State University Museum of Zoology (LSUMZ) (No. 116908). A total of 6 males and 4 females of this new species are all at LSUMZ. So far, *H. parkeri* is known only from the type locality, an ecologically heterogeneous area consisting of a savanna-like habitat, a low-diversity ridge-top habitat on sandy soil, a semi-stunted forest, and a tall cloud forest on good soil. "*H. parkeri* was noted most commonly in the canopy and midlevels of the tallest forest" (Davis & O'Neill 1986: 343). It also occurred in other habitats, but less commonly. *H. parkeri* was often found in mixed flocks with other Formicariidae, Furnariidae and Tyrannidae.

Davis & O'Neill (1986) argued that several taxa of *Herpsilochmus*, hitherto considered to be subspecies of *H. pileatus*, ought to be treated as distinct, allopatric species. *H. parkeri* is geographically closest to *motacilloides*. The various allopatric taxa of this group of species within *Herpsilochmus* vary slightly in both morphological and vocal characters, but not enough data exist as yet about vocalizations. Davis & O'Neill (1986: 350–351) considered the question of subspecific *vs*. specific identity of the allopatric trio *H. parkeri, H. motacilloides* and *H. atricapillus*, and believed that species status is the better alternative at present. Furthermore, they "hesitate to classify them [these 3 species plus *H. pileatus*] formally in a single superspecies until the ranges of *H. pileatus* and *H. atricapillus* are better known" (Davis & O'Neill 1986: 351). Sibley & Monroe (1990: 386) included *parkeri, motacilloides, atricapillus* and *pileatus* in a single superspecies.

It seems to us that it is not possible to decide on species status at present. *H. parkeri* may be treated as a subspecies of *pileatus* or as a member of the [*pileatus*] superspecies; for the time being we favour the former (Bb).

(33) *Terenura sicki* Teixeira & Gonzaga 1983b, *Bull. Brit. Orn. Cl.* 103: 133—"Serra Branca", Murici, Alagoas, northeastern Brazil (c. 9°15′S, 35°50′W).

= *Terenura sicki* (Ab).

This new antbird was originally described on the basis of a single female collected in 1979 and deposited in the MNRJ, number 32048 (Texeira & Gonzaga 1983b). Further work has permitted the collection of 5 additional specimens in 1983 (3 males and 2 females, all in the MNRJ), and one sub-adult and one adult male (both also in MNRJ) in 1987 (Teixeira *et al.* 1988). The holotype is now identified by Teixeira (1987b) as an immature female.

The new taxon is known on the basis of specimens from the type locality (Serra Branca, Murici, Alagoas) and from Quebrangulo, Alagoas, and from sight records from Novo Lino, Alagoas. The only illustration of the new species is a black and white figure of 3 specimens in Teixeira (1987b: 244). Details about plumages, habitat, relative abundance, behaviour, vocalization and breeding are given in Teixeira (1987b). The male resembles in plumage colour and pattern several species of *Myrmotherula*. The female is said to differ from other species of *Terenura* by its orange underparts. Nowhere is it clearly indicated why the new taxon was placed in *Terenura*.

Remsen (*in litt.*), Fitzpatrick (*in litt.*), Sick (*in litt.*) and Ridgely (*in litt.*) all thought that *T. sicki* is a valid new species. Sick and Ridgely (*in litt.*) stated that it is close to *T. maculata*, forming a superspecies with it. Sibley & Monroe (1990: 388) accepted *T. sicki* as a full species (not in a superspecies with *T. maculata*).

It seems to us that a comparative study of the type series of *T. sicki* with a number of other small Formicariidae should be undertaken before the generic status of this form can be fully confirmed. Pending further reviews, we accept *T. sicki* tentatively as a new species (Ab).

(34) *Cercomacra manu* Fitzpatrick & Willard 1990, *Auk* 107(2): 239—12 river km downstream from Shintuya on left bank of Alto Rio Madre de Dios, Dept. Madre de Dios, Perú, 12°33′S, 71°17′W, altitude 420 m.

=*Cercomacra [melanaria] manu* (Ac); or *Cercomacra [nigricans] manu* (Ac).

A total of 14 males and 10 females of this new antbird was examined (deposited in the LSUMZ, FMNH and AMNH). The holotype, an adult female, is number 310653 in the FMNH. *C. manu* is a member of the '*Cercomacra nigricans*' species group, including 4 allopatric species-level taxa besides *manu*: *nigricans, carbonaria, ferdinandi* and *melanaria*. *C. manu* occurs in bamboo habitats (illustrated by photographs) in Perú (Depts. Cuzco, Ucayali and Madre de Dios) and Bolivia (Dept. Pando). The males of the taxa of the '*nigricans*' group are very similar to one another, but the females are more distinct (a colour plate accompanied the original description). On the basis of several "shared characteristics we hypothesize that *manu* and *melanaria* are sister taxa, possibly close enough to be recognized as a superspecies" (Fitzpatrick & Willard 1990: 243). *C. manu* and *C. melanaria* are allopatric, but their geographical disjunction is not nearly as large as that among the other members of the '*nigricans*' group. We would include *manu* as an allospecies of either the *C. [melanaria]* superspecies (if only *C. manu* and *C. melanaria* are included as members), or of the *C. [nigricans]* superspecies (if all allopatric members of this 'group' are included); hence Ac in the classification.

(35) *Grallaria carrikeri* Schulenberg & Williams 1982, *Wilson Bulletin* 94(2): 105—Cordillera Colán, SE La Peca, c. 5°34′S, 78°19′W, altitude 2450 m, Dept. Amazonas, Perú.

=*Grallaria [nuchalis] carrikeri* (Ac).

The type series of this new species consists of 13 specimens, one in the Delaware Museum of Natural History and all the others in the LSUMZ. The holotype is an adult male (number 88044 at LSUMZ). A colour illustration accompanies the original description. *G. carrikeri* is known from 3 localities in the northern Peruvian Andes: Cordillera Colán (Dept. Amazonas), near Ingenio on the road to Laguna Pomacochas (Dept. Amazonas), and Cumpang, near Ongón (Dept. La Libertad). *G. carrikeri* is closely related to the allopatric *G. nuchalis*. The 2 forms are separated by the low and dry valley of the Rio Marañón. The morphological differences (especially whitish bill) and vocal differences (including data from some playback experiments) suggested to Schulenberg & Williams (1982: 111) that "*G. carrikeri* has achieved species status". Wiedenfeld (1982) has described the nest of *G. carrikeri* and discussed the nests of antpittas. Fitzpatrick (*in litt.*), Graves (*in litt.*), Remsen (*in litt.*) and Ridgely (*in litt.*) all believe that *G. carrikeri* is a valid species belonging in a superspecies with *nuchalis*. Sibley & Monroe (1990: 417) also placed *nuchalis* and *carrikeri* in the *G. [nuchalis]* superspecies. We accept this view here and classify *carrikeri* as Ac.

(36) *Grallaria blakei* Graves 1987, *Wilson Bulletin* 99(3): 314—east slope of the Cordillera Carpish, near the Carretera Central, c. 2400 m. altitude, Department of Huánuco, Perú.
= *Grallaria blakei* (Ab).

This new species, described on the basis of 8 specimens (one in the FMNH and 7 in the LSUMZ) occurs at 3 localities along the eastern Peruvian Andes in the Departments of Huánuco and Amazonas, between 2135 and 2470 m. At Cordillera Carpish and Cordillera Colán, where *G. blakei* has been collected nearly sympatrically with the very similar and widespread *G. rufula*, "a distributional hiatus is found between their known elevational ranges" (Graves 1987: 320). Graves (1987: 320) added that "whether this gap is real or an artefact of sampling is not known". The holotype (adult female) is number 64228 in the LSUMZ. A colour plate of *G. blakei* accompanied the original description. *G. blakei* differs slightly from *G. rufula* in colour and size.

Sibley & Monroe (1990: 418) listed *G. blakei* as a full species. However, as Graves (1987) himself pointed out, more evidence is needed on the status of these 2 forms in their contact areas. For the time being, we classify *G. blakei* as Ab, but look forward to more corroborating evidence.

(37) *Grallaricula ochraceifrons* Graves, O'Neill & Parker 1983, *Wilson Bulletin* 95(1): 1—10 km (by road) below (NE) Abra Patricia, altitude c. 1890 m (6200 ft), 5°46'S, 77°41'W, Depto. San Martín, Perú.
= *Grallaricula [peruviana] ochraceifrons* (Ac).

The holotype (LSUMZ number 81998) is an adult male. The type series consists of 5 specimens (all at LSUMZ) collected at 2 localities in northern Perú (Depts of San Martín and Amazonas), at altitudes from 1890 to 1980 m. A colour plate and a black and white photograph of a live, hand held bird, accompany the original description. *G. ochraceifrons* is sexually dimorphic (although only 1 ♀ has been collected to date). *G. peruviana*, which is allopatric with *G. ochraceifrons* and separated from it by the dry Marañón Valley, is also sexually dimorphic. Unfortunately the vocalizations of *G. ochraceifrons* are unknown. Tentatively, Graves *et al.* (1983: 4) suggested that *G. peruviana* and *G. ochraceifrons* are members of the same superspecies. Graves (*in litt.*) wrote that *G. ochraceifrons* was "perhaps superspecifically related to either *G. lineifrons* or *G. peruviana*". Fitzpatrick (*in litt.*) thought *G. ochraceifrons* to belong in a superspecies with *G. peruviana*. Sibley & Monroe (1990: 419) placed *peruviana* and *ochraceifrons* in the *G. [peruviana]* superspecies. We treat it here as Ac, but more evidence (specimens, vocalizations) is clearly needed.

Rhinocryptidae

(38) *Scytalopus psychopompus* Teixeira & Carnevalli, 1989, *Bol. Mus. Nac., Nov. Ser., Zool.*, no. 331: 2—Valença, Bahia, Brazil.
= *Scytalopus [indigoticus] psychopompus* (Ac).

Based on 3 specimens, 2 housed in the MNRJ and one in the Museu de Zoologia of the University of São Paulo (one adult female holotype, MN number 34371, and 2 males), this new species has been collected at Valença, Bahia and Ilhéus, Bahia, in northeastern Brazil. *S. psychopompus* is allopatric with the widespread *S. indigoticus*. A photograph in the original description shows the 2 species (female specimens) side by side. *S. psychopompus* differs from *S. indigoticus* in having uniform (unbarred) chestnut on the flanks and crissum. *S. psychopompus* was compared with a large series of *S. indigoticus*, which shows a substantial amount of individual variation, but which always seems to have barring on the crissum or flanks. Tentatively we list *S. psychopompus* as an allospecies of *S. [indigoticus]* (Ac). Much more information on individual variation and especially new data on voice are needed for the Bahia populations. *Scytalopus* is a notoriously difficult genus.

Tyrannidae

(39) *Phylloscartes ceciliae* Teixeira 1987a, *Bull. Brit. Orn. Cl.* 107(1): 38—'Serra Branca', Murici, Alagoas, northeastern Brazil (c. 9°15′S, 35°50′W), altitude 550 m.

= ? *Phylloscartes ceciliae* (Ba).

Described on the basis of 5 specimens collected in 1983 and 1984 (Teixeira 1987a), to which were added 4 specimens collected in 1987 (Teixeira *et al.* 1988), this new species occurs in Alagoas (2 localities). All specimens are in the MNRJ. The holotype, an adult male, is number 34041. It is not clear to what other species of *Phylloscartes (sensu stricto* or *sensu lato*?) the putative new species has been compared, since the original description does not indicate what comparative material (if any) was used. A black and white line drawing in the original description is the only illustration of *P. ceciliae*. Sibley & Monroe (1990: 347) accepted *P. ceciliae* as a valid species.

Given the difficulties of Tyrannidae systematics, and the very incomplete nature of the description, however, we feel that we do not have enough information about *P. ceciliae* at present for us to classify it as anything but a *species inquirenda* (Ba).

(40) *Phylloscartes lanyoni* Graves 1988, *Wilson Bulletin* 100(4): 529—El Pescado, 12 km below Pto. Valdivia on the Río Cauca, c. 1500–1700 ft [457–518 m], Department of Antioquia, Colombia.

= ? *Phylloscartes lanyoni* (Ba).

Known only from the holotype, an adult male at the USNM, Washington, DC (number 402716), the type locality of this new *Phylloscartes* is distant from the ranges of *P. venezuelanus* and *P. orbitalis* (colour plate in original description). As Graves (1988: 532) himself stated: "Based on the similarity of body plumage and reduced auricular spot, *P. lanyoni* appears to be a trans-Andean relative of *P. orbitalis*, although a close relationship to *P. venezuelanus* and *P. gualaguizae* is possible." Given this uncertainty, Sibley & Monroe's (1990: 346) inclusion of this species in a superspecies with *P. orbitalis* appears premature.

Further research on song and other characteristics is needed to determine the rank of these forms. Owing to the great similarity of species in this genus it is difficult to decide whether allopatric populations should be ranked as subspecies or allospecies. We classify it conservatively here as a *species inquirenda* (Ba).

Troglodytidae

(41) *Thryothorus eisenmanni* Parker & O'Neill, 1985, *American Orn. Union, Orn. Monogr.* no. 36: 9—San Luis on Ollantaitambo-Quillabamba road, above Huyro, 13°06′S, 72°25′W, altitude '9000 feet' [2744 m], Department of Cuzco, Perú.

= *Thryothorus euophrys eisenmanni* (Bb).

Based on 16 specimens, all at the LSUMZ except one (at the AMNH), this new wren is closely related to *T. euophrys*. *T. eisenmanni* occurs from 1830 to 3350 m in montane forest with dense bamboo thickets, apparently its favoured habitat, in the Department of Cuzco (eastern Peruvian Andes). The holotype is an adult male (LSUMZ number 78913). A colour plate accompanied the original description.

Some playback experiments showed that *T. euophrys atriceps* individuals respond much more strongly to songs of *T. euophrys longipes* than to songs of *T. eisenmanni*, "which supports our taxonomic decision to regard *eisenmanni* as a full species" (Parker & O'Neill 1985: 12). Ridgely (*in litt.*) suggested that *T. eisenmanni* is "close to *euophrys*". Graves (*in litt.*) and Fitzpatrick (*in litt.*) would put *T. eisenmanni* as "allospecies of *T. euophrys*". Sibley & Monroe (1990: 560) treated *euophrys* and *eisenmanni* as members of the *T. [euophrys]* superspecies. We believe, however, that *eisenmanni* is a well-marked subspecies of *euophrys*, and treat it tentatively as Bb here.

Emberizidae (Thraupinae)

(42) *Tangara meyerdeschauenseei* Schulenberg & Binford 1985, *Wilson Bulletin* 97(4): 413—2 km northeast of Sandia, c. 2175 m altitude, 14°17′S, 69°26′W, Department of Puno, Perú.

= *Tangara [cayana] meyerdeschauenseei* (Ac).

Based on 4 specimens in the LSUMZ (2) and the MNHN, (2), this new *Tangara* occurs in the Andes of southeastern Perú (Dept. Puno). The holotype is an adult male, number 98917 in LSUMZ. A colour plate accompanied the original description. This montane *Tangara* is clearly a member of the group of species of the "*cayana* group", including taxa *flava, cucullata* and *vitriolina*. *T. meyerdeschauenseei* differs from these other taxa in several characters, including the lack of orange or rufous-buff crown.

Sibley & Monroe (1990: 755) accepted *meyerdeschauenseei* as a valid species but did not include it in any superspecies. Other workers, however, feel that this species is closely allied to other allopatric species. Graves (*in litt.*) thought that *T. meyerdeschauenseei* was "probably an allospecies of *T. vitriolina*". Fitzpatrick (*in litt.*) thought that it belonged in the same superspecies as *cayana* and *vitriolina*. Ridgely (*in litt.*) also felt that it belonged "clearly in the *cayana* complex". We list it here as a member of the *T. [cayana]* superspecies (Ac).

(43) *Tangara phillipsi* Graves & Weske 1987, *Wilson Bulletin* 99(1):1—Cerros del Sira, 9°26′S, 74°45′W, 1300 m altitude, Departamento de Huánuco, Perú.
= *Tangara heinei phillipsi* (Bb).

The holotype is deposited at the AMNH (No. 820969). One other specimen is at the AMNH, and 2 more at the Zoological Museum of the University of Hamburg, Germany. The new species is darker than, but otherwise is quite similar to, allopatric *T. heinei*. Graves & Weske (1987: 4) placed *heinei* and *phillipsi* in the same superspecies, and Sibley & Monroe (1990: 756) adopted this procedure. We feel that *phillipsi* is not very different from *heinei* and therefore might be considered a subspecies of *T. heinei*. We so consider it here (Bb).

DISCUSSION

Of the 43 species described as new in 1981–1990, 24 (58%) can be considered good species. Of these 24 species, 13 (54%) belong to superspecies. An average of 2.4 good new species per year were thus described in 1981–1990. This rate is identicial to the figure for the 5-year period 1976–1980. Earlier average figures are 3.1/year for 1966–1975, 3.5/year for 1956–1965, 2.6/year for 1941–1955, and 6.0/year for 1938–1941. 162 good new species of birds have been described in the 52 years from 1938–1990, a rate of about 3.1/year.

In 1981–1990, one new species has been reduced to the synonym of an already known species. We consider 8 of the new species as probably subspecies of already known species. Finally, 10 species are kept here tentatively as *species inquirenda* pending further research into their status.

Even though our summary above seems to indicate that the new species can easily be assigned to a given category, in practice many uncertainties still exist. In particular many new species belong to allopatric groups of taxa which on present evidence could be considered either as allospecies or subspecies. In the text we have taken some pains to point out these difficulties, thereby hoping to spur further needed new research on these forms. We would like to stress here the importance of having more specimens and more complete data in hand before descriptions are attempted. We present specific guidelines for species descriptions in a separate paper in this volume.

SUMMARY

A total of 43 species of birds was described as new in the 10 year period from 1981–1990. Of these, 24 can be considered 'good' species:

Aa New species in new genera: None.
Ab New species not clearly members of a superspecies (11): 5, 7, 9, 11, 16, 18, 21, 22, 26, 33, 36.
Ac Allospecies (members of a superspecies) (13): 2, 10, 12, 17, 20, 23, 24, 31, 34, 35, 37, 38, 42.

An additional 19 names cannot now be assigned the status of valid full species:

Ba *Species inquirendae* (10) 3, 4, 6, 8, 19, 25, 29, 30, 39, 40.
Bb Subspecies (8): 1, 13, 15, 27, 28, 32, 41, 43.
Bc Synonyms (1): 14.
Bd Invalid names: none.

Acknowledgements

We acknowledge our debt to the following colleagues, who generously made critical comments and helped us greatly during the preparation of this review: Dean Amadon, Allison V. Andors, John Ash, Richard C. Banks, Bruce Beehler, Robert Bleiweiss, Walter Bock, Walter E. Boles, W. Ralph Browning, John Cox, Jared Diamond, Jean Dorst, Christian Erard, John Fitzpatrick, Gary Graves, Philip Humphrey, Ned Johnson, C. Jouanin, Allen Keast, Stuart Keith, Ben King, Scott Lanyon, Manuel Nores, Storrs Olson, Shane Parker, Kenneth Parkes, Robert Ridgely, Richard Schodde, Lester Short, the late Helmut Sick, David Snow, Melvin Traylor, Jr., Van Remsen and Richard Zusi. We are grateful to Helen Kwon and Elizabeth De Jesus who typed the manuscript, and to James Monk for his careful editing of the manuscript.

APPENDIX I

Alphabetical list of the 43 putative new species described from 1981 to 1990 (Numbers in parenthesis refer to the species' number in the text.)

Amazona kawalli (25)
Asthenes luizae (29)
Batis occultus (15)
Calidris paramelanotos (3)
Caprimulgus prigoginei (5)
Cercomacra manu (34)
Cettia carolinae (11)
Cichlornis llaneae (12)
Clytoctantes atrogularis (31)
Diomedea amsterdamensis (1)
Gerygone ruficauda (14)
Glaucidium albertinum (4)
Grallaria blakei (36)
Grallaria carrikeri (35)
Grallaricula ochraceifrons (37)
Herpsilochmus parkeri (32)
Hirundo perdita (8)
Malurus campbelli (13)
Melignomon eisentrauti (6)
Meliphaga hindwoodi (17)
Mirafra ashi (7)
Nectarinia rufipennis (16)
Otus hoyi (27)
Otus marshalli (26)
Otus petersoni (28)
Philydor novaesi (30)
Phyllastrephus leucolepis (9)
Phylloscartes ceciliae (39)
Phylloscartes lanyoni (40)
Ploceus burnieri (18)
Ploceus ruweti (20)
Ploceus victoriae (19)
Pyrrhura orcesi (24)
Rallus okinawae (2)
Scytalopus psychopompus (38)
Stachyris latistriata (10)
Tachyeres leucocephalus (23)
Tangara meyerdeschauenseei (42)
Tangara phillipsi (43)
Terenura sicki (33)
Thryothorus eisenmanni (41)
Vidua larvaticola (22)
Vidua raricola (21)

APPENDIX II

SPECIES OMITTED IN EARLIER ACCOUNTS

OLD WORLD

Phasianidae

Lophura hatinhensis Vo Quy 1975, *Birds of Vietnam*: 245.
= ? *Lophura hatinhensis* (Ba).

The single existing specimen of this new taxon (a male, no number or place of deposition are given in the description) was compared to closely related pheasants "like *L. imperialis* Delacour and Jabouille, *L. edwardsi* Oustalet in Viet Nam, *L. inornata* Salvadori in Sumatra and *L. swinhoei* Gould in Taiwan". The new species is "closest to *L. edwardsi* the only difference is [*L. edwardsi*] has darker color, there is no shiny green [in the upper wing coverts] and there are no middle four white tail feathers". Measurements: "wing 245; tail 270; feet 89; beak 30 mm. Weight 1100 g."

We overlooked this species in the account for the period 1966–1975 (Mayr & Vuilleumier 1983), as pointed out to us by King (pers. comm.). It has been extremely difficult for us to obtain copies of the original description. We are grateful to Craig Robson for sending us a copy of this description and to Toan Nguyen for translating it.

Recent accounts in the western literature include that of Collar & Andrew (1988: 38), who stated that this species is "only known from a small area south of Vinh in several adjacent valleys on the eastern slopes of the mountains, preferring lower altitudes than Edwards' Pheasant *L. edwardsi*". Robson *et al*. (1989: 76) stated that *Lophura hatinhensis* "is only known to occur in the vicinity of the type-locality: Song Tund, and adjacent Ky Thuong sub-district". They added: "The original and only (existing) specimen was collected in 1964 by the late Do Ngoc Quang. A second specimen was collected from Ky Thuong sub-district in 1974 by T. V. L. [Truong Van La], but was not preserved in its entirety." A popular account has been published in German (see Bahr & Nguyen 1992) including a photograph in colour of a living bird in the Hanoi zoo.

In the absence of further information, we feel we cannot comment on whether *Lophura hatinhensis* is a recognizable species. As an allopatric population closely related to *L. edwardsi*, *L. hatinhensis* might be considered either as a subspecies or an allospecies. Until further information is available, upon which to base a decision, we prefer to classify it as Ba.

Caprimulgidae

Nyctisyrigmus kwalensis, Davis 1978, *Pan American Studies* 1(2): 47—Kwale, SE Kenya.
= ? *Caprimulgus pectoralis* (Bd).

This new species and the next (*Allasma northi*) were omitted from the 1976–1980 account (Vuilleumier & Mayr 1987), and we thank Ralph Browning for bringing them to our attention.

Nyctisyrigmus kwalensis was described on the basis of tape recordings of songs. We quote from Davis (1978: 47): "Diagnosis: External morphological characters are the same as those of other members of the *Caprimulginae* (sic). The species specific song is a typical two figure phrase of the genus *Nyctisyrigmus* in which the terminal portion of the second figure shows frequency modulation." And further: "The type song phrase specimen is listed under 'species with whistling songs' and is number '4' of the 'Dusky or South African Nightjar—*Caprimulgus pectoralis*' group in the Myles North papers. North gave credit for the recording to Keith and said it was from Kwale, SE Kenya and made in 1961."

This name is thus based exclusively on a sonagram. It is a *nomen nudum*, a conclusion that agrees with that reached by Browning & Richard Banks (*in litt.*).

Allasma northi, Davis 1978, *Pan American Studies*, 1(2): 52—no type locality given.
= ? *Caprimulgus clarus* (Bd).

"The type song phrase specimen is listed as number '4' in the group of recordings discussed under: 'SLENDER-TAILED NIGHTJAR'—*Caprimulgus clarus* Reichnow (sic). This heading comes on page 5 of the unpublished paper: AN INVESTIGATION OF THE SONGS OF THE NIGHTJARS OF EAST, CENTRAL AND SOUTH AFRICA, by Myles E. W. North. The paper is rather widely circulated and is found in various Museums" (Davis 1978: 52).

Described solely on the basis of sonagrams, as was the previous species, this new name is a *nomen nudum* without nomenclatural validity. We agree in this with Browning & Banks (*in litt.*).

APPENDIX III

TAXA MENTIONED AS POTENTIAL NEW SPECIES IN THE PERIOD 1981–1990 BUT NOT FORMALLY DESCRIBED

We list below 2 taxa that have been mentioned in the literature as new or potentially new, but that the authors have refrained from naming as new species. Note that this listing does not pretend to be complete, as we cite only those papers that have come to our attention during our search for new species' descriptions. We include these accounts here only to warn ornithologists who might be tempted to designate such populations as new species in the future, that they must do so in professional fashion, with a precise description and designation of type specimens.

OLD WORLD

Muscicapidae (Sylviinae)

Phylloscopus sp.

Alström *et al.* (1990) heard and saw *Phylloscopus* warblers in Sichuan Province and Hebei Province, China, in 1986, 1988 and 1989, that were distinct from *P.* (*p.*) *chloronotus* (for taxonomy of *P. proregulus* and *P.* (*p.*) *chloronotus* see Alström & Olsson 1990). No specimens were obtained. On the basis of visual and voice observations, the differences between "*Phylloscopus* sp." and *P. chloronotus* were listed. Playback tests of *P.* (*p.*) *chloronotus* vocalizations showed "no response whatsoever to the *P.* sp. song and 'calls', but a very strong aggressive response to its own song" (Alström *et al.* 1990: 45–46).

We wish to compliment the authors for their restraint. Despite extensive field experience with the 'new' taxon, they declined formally to name it until specimens are collected.

NEW WORLD

Trochilidae

Patagona sp.

Fjeldså & Barbosa (1983) suggested that a new species of *Patagona* occurs in the Andes of NE Colombia, based on the observations of a single bird in October 1981. Such an occurrence would be of interest, since *Patagona* currently has a single species, *gigas*, and since this would represent a northward extension of 900 km as well as an ecological shift. After careful study of the Fjeldså & Barbosa (1983) paper, Robert Bleiweiss and one of us (F.V., unpub. ms.) believe that there is not enough evidence to warrant the suggestion of a new species of *Patagona*. No specimen of the purported new taxon was collected, and the informal description of the putative new form is not a diagnosis and does not even permit unquestionable generic assignment. In fact, the information provided by Fjeldså & Barbosa (1983) is equally consistent with the identification of the observed bird as a female *Pterophanes* in slightly unusual plumage. *Pterophanes* is the second largest hummingbird, close to *Patagona* in size, and is known to occur in the region where the purported *Patagona* was observed.

Only a few characters of the described bird indicate that it could be a *Patagona*. These include light undertail coverts, and a non-uniform tail colour, darkest distally. No mention is made, however, of the rump, which is uniquely white in all known *Patagona* populations and could thus serve as a diagnostic feature. Other characters are equally consistent with either *Patagona* or *Pterophanes*: long forked tail, and slow wingbeat. The majority of characters suggest *Pterophanes*. Fjeldså & Barbosa (1983) claim that female *Pterophanes* have extensive green discs on rufous underparts, but female *Pterophanes* in the collection of the AMNH have uniform rufous underparts, as in the bird they described. The dark back with a green lustre, and a straight bill, thinner than that of *Patagona*, are also both characteristic of *Pterophanes*.

Plumage variants and morphs are not uncommon in the Trochilidae. This possibility should be considered before any attempt at a formal taxonomic description of this bird is made. Until such time as specimens are collected, Bleiweiss and Vuilleumier advise that the suggestion of a new species of *Patagona* be disregarded.

APPENDIX IV

ADDITIONAL NOTES ON 13 SPECIES REPORTED IN PREVIOUS ACCOUNTS

We comment below on 13 species described in earlier accounts (Mayr 1971, Mayr & Vuilleumier 1983, Vuilleumier & Mayr 1987) and for which new information has appeared in the literature since our earlier reviews.

OLD WORLD

Turdidae

Zoothera kibalensis = ?*Zoothera kibalensis*

In the instalment for the years 1976–1980 Vuilleumier & Mayr (1983: 138) treated *Z. kibalensis* (Prigogine 1978) "as a *species inquirenda* pending either further specimens or life history information". In a later paper, Prigogine (1989: 189) reported that a recent search for this bird had failed, but that "it is possible that this ground-thrush will be recorded finally when the search will be extended in a convenient biotype, at an altitude near 1,500 metres". Prigogine stated that the 2 specimens of *kibalensis* "have nothing in common with . . . *Zoothera princei*", that *kibalensis* is heavier than *Z. camaronensis graueri*, and that the characters of the 2 specimens of *kibalensis* are such as to rule out hybridization between *cameronensis* and *princei*. He concluded: "For these reasons *Z. kibalensis* must be retained as a good species" (Prigogine 1989).

Keith (pers. comm.), who is editing *Zoothera* for Vol. 5 of *The Birds of Africa*, does not intend to treat it as a valid species unless further evidence is forthcoming on voice and behaviour. R. J. Dowsett (pers. comm. to Keith) does not believe *Z. kibalensis* to be a good species, and it does not appear in his forthcoming *Checklist of Afrotropical Birds*. We prefer to retain it as a *species inquirenda* for the time being, as did Sibley & Monroe (1990: 511).

Sittidae

Sitta ledanti = *S. [krueperi] ledanti*

Bellatreche & Chalabi (1990) and Bellatreche (1991) have reported new localities for this new nuthatch (Vielliard 1976), which is not restricted to *Abies numidica* habitats as was previously believed, but also occurs in 3 other areas between 900 and 1400 m in oak (*Quercus canariensis* and *Q. afares*) woodlands. The 4 locations are: Djebel Babor (2300 ha.), Guerrouch Forest (10,500 ha.), Tamentout Forest (9600 ha.) and Djimla Forest (1000 ha.). The population size of this nuthatch is therefore larger than once thought, and its habitat requirements more varied.

NEW WORLD

Cracidae

Crax estudilloi = ?*Crax estudilloi*

The saga of *Crax estudilloi* Allen *et al.* (1977), reported by Vuilleumier & Mayr (1987) in the 1976–1980 instalment, continues. The bird died when still not fully adult, and much effort was expended to send the specimen frozen to Louisiana State University Museum of Zoology. Unfortunately, it arrived in a decomposed state, and it was possible to save only the skeleton and a few feathers—LSUMZ No. 140000 (V. Remsen, pers. comm.).

Remsen & Traylor (1989: 56) discussed this bird and concluded: "Although a number of cracid experts feel that this bird represents a valid species, we remain cautious until a thorough analysis of the specimen is completed; therefore, we follow Vuilleumier & Mayr (1987) in listing this as a *species inquirenda*." Sibley & Monroe (1990: 9) regarded it "as a likely hybrid between *C. fasciolata* and some other *Crax* species".

Trochilidae

In the 1976–1980 instalment Vuilleumier & Mayr (1987) gave additional information on 6 putative new species of hummingbirds in the genera *Threnetes* (3 species) and *Phaethornis* (3 species) that they had reviewed previously (Mayr & Vuilleumier 1983). We provide below some additional comments resulting from useful critical studies by Hinkelman (1988a, 1988b).

Threnetes cristinae = Threnetes leucurus loehkeni.

In an earlier paper (Mayr & Vuilleumier 1983) it was suggested that *T. cristinae* Ruschi (1975) was likely to be a "synonym of *Threnetes* (*?leucurus*) *loehkeni*". Hinkelmann's (1988b) discussion makes it clear that "there remains little doubt that '*T. cristinae*' is merely a synonym of *Threnetes leucurus loehkeni*".

Threnetes loehkeni = Threnetes leucurus loehkeni

In an earlier account (Mayr & Vuilleumier 1983) it was thought that *T. loehkeni* Grantsau (1969) was a subspecies of *leucurus*, but later Vuilleumier & Mayr (1987) concluded that *loehkeni* was a recognizable species. Grantsau (in Vuilleumier & Mayr 1987) thought that *Threnetes niger freirei* is the adult of "*T. loehkeni*". Hinkelmann (1988b) concluded that "until more recently collected *Threnetes* specimens are available from Amapá, Brazil, and from French Guiana, the taxonomic affinities between *T. niger* and *T. leucurus* remain obscure, and the best treatment of *loehkeni* for the present is as a distinctive subspecies of *T. leucurus*". We concur.

Threnetes grzimeki = Glaucis hirsuta

That *T. grzimeki* Ruschi (1973b) is a synonym of *Glaucis hirsuta*, an opinion reached earlier by Vuilleumier & Mayr (1987), is in agreement with Hinkelmann (1988b).

Phaethornis margarettae = Phaethornis malaris margarettae

P. margarettae Ruschi (1972), based on the 10 specimens available to Ruschi and an additional 8 specimens listed by Hinkelmann (1988b), is not easy to define. Hinkelmann (1988b), after a review of the evidence, concluded that he agrees (with various authors) "in considering *margarettae* a subspecies of the *P. superciliosus/malaris* species group but prefer[s] to treat it as *P. malaris margarettae* until further information concerning its relationship to *P. malaris insignis* is available". This seems a wise suggestion to us.

Phaethornis nigrirostris = Phaethornis eurynome eurynome

The question of the status of *P. nigrirostris* Ruschi (1973a) seems to have been solved by Hinkelmann (1988b): "I consider '*P. nigrirostris*' to represent aberrant black-billed individuals occurring within the *P. eurynome* population in the Nova Lombardia Reserve, Espirito Santo, Brazil."

Phaethornis maranhaoensis = Phaethornis nattereri

In 1983 Mayr & Vuilleumier had listed *P. maranhaoensis* Grantsau (1968) as *species inquirenda*, and in 1987 Vuilleumier & Mayr accepted Grantsau's view of specific distinctness. Hinkelmann (1988a) carried out a detailed study of *maranhaoensis* and concluded that "the description of *Phaethornis maranhaoensis* Grantsau 1968 is based on the previously undescribed male plumage of *Phaethornis nattereri* Berlepsch 1887; *P. maranhaoensis* should, therefore, be regarded as synonymous with *P. nattereri*". We agree with Hinkelmann (1988a).

Furnariidae

Cinclodes olrogi = ?Cinclodes fuscus olrogi

Vuilleumier & Mayr (1987) discussed *Cinclodes olrogi* Nores & Yzurieta (1979) and concluded: "We tentatively list this species as an allospecies of *oustaleti*, but we are aware that a thorough comparative study of *Cinclodes* spp. carried out in the Sierra de Córdoba and in the Andes of Argentina might modify this conclusion". Nores (1986) described a new subspecies (*riojanus*) of *Cinclodes fuscus* from La Rioja, and compared this new taxon to several other subspecies of *fuscus* (*albiventris, tucumanus, rufus* and *yzurietae*) and to *olrogi*. Resemblances between *C. fuscus riojanus* and *C. olrogi* prompted Nores (1986) to conclude that "*C. olrogi* is not a species, but a subspecies of *C. fuscus*, a species which has differentiated into several subspecies in the montane zone of Argentina, especially in the Sierras Pampeanas". Unfortunately, Nores (1986) did not compare *olrogi* to *C. oustaleti*. Although it now seems more likely to us that *olrogi* belongs to *C. fuscus* than to *C. oustaleti*, as we had believed earlier, we still feel the need for more study. It is retained as an allospecies by Sibley & Monroe (1990: 395).

Philydor hylobius = Automolus roraimae

Mayr (1971), in the new species instalment for 1956–1965, considered *Philydor hylobius* Wetmore & Phelps (1956) as a valid species, "similar to and related to *P. atricapillus*", and classified it as Ad (allospecies which some authors would consider merely subspecies). Recent collections in the Cerro de la Neblina area did not include new material of this taxon. Additional material of *Automolus roraimae*, however, permitted Dickerman *et al.* (1986) to conclude that the juvenile *Philydor hylobius* in the USNM was 'inseparable' from juvenile *Automolus roraimae*, and that the adult *Philydor hylobius* (the type) "is actually an erythristic specimen of *A. roraimae*". Thus "*Philydor hylobius* Wetmore and Phelps should be considered a junior synonym of *Automolus roraimae* Hellmayr" (Dickerman *et al.* 1986: 431).

Tyrannidae

Serpophaga griseiceps = *Serpophaga subcristata munda*

Serpophaga griseiceps Berlioz (1959), which Mayr (1971) had considered as a new species not clearly a member of a superspecies, "very similar to *munda*", is actually a synonym of *S. subcristata munda* (Traylor 1979: 41). Sibley & Monroe (1990: 344) treat *munda* as a distinct species (*fide* J. V. Remsen) on the basis of differences in vocalizations between it and *subscristata.*

Todirostrum albifacies = *Poecilotriccus tricolor*

T. albifacies Blake (1959), reviewed by Mayr (1971) and considered as a full species in the superspecies *T. capitale*, is in fact a synonym of *Poecilotriccus tricolor* (Traylor 1979: 77).

References:

Allen, G. A. Jr., Allen, G. A. III & Allen, L. 1977. A new species of currasow discovered. *Game Bird Breeders, Avicult. Zool. Conserv. Gaz.* 26 (6): 6–7.

Alström, P., Colston, P. R. & Olsson, U. 1990. Description of a possible new species of leaf warbler of the genus *Phylloscopus* from China. *Bull. Brit. Orn. Cl.* 110: 43–47.

— & Olsson, U. 1990. Taxonomy of the *Phylloscopus proregulus* complex. *Bull. Brit. Orn. Cl.* 110: 38–43.

Amadon, D. 1966. The superspecies concept. *Syst. Zool.* 15: 245–249.

Ash, J. S. 1986. A *Ploceus* sp. nov. from Uganda. *Ibis* 128: 330–336.

— 1987. *Ploceus victoriae. Ibis* 129: 406–407.

Bahr, N. & Nguyen, C. 1992. Der Vo Quy-Fasan. *Ornis* 3: 12–13.

Baker, N. E. & Baker, E. M. 1990. A new species of weaver from Tanzania. *Bull. Brit. Orn. Cl.* 110: 51–58.

Bellatreche, M. 1991. Deux nouvelles localisations de la Sitelle [sic] kabyle *Sitta ledanti* en Algérie. *L'Oiseau et R. F. O.* 61: 269–272.

— & Chalabi, B. 1990. Données nouvelles sui l'aire de distribution de la Sitelle [sic] kabyle *Sitta ledanti. Alauda* 58: 95–97.

Beno, M. 1982. What steams, fights and doesn't fly? *Ducks Unlimited*, July/Aug: 30–34.

Berlioz, J. 1959. Description de deux espèces nouvelles d'Oiseaux de Bolivie. *Bull. Mus. Hist. Nat. Paris* 31(2): 217–219.

Blake, E. R. 1959. A new species of *Todirostrum* from Peru. *Nat. Hist. Misc., Chicago,* No. 171.

Bourne, W. R. P. 1989. The evolution, classification and nomenclature of the great albatrosses. *Gerfaut* 79: 105–116.

Brazil, M. A. 1991. *The Birds of Japan.* Smithsonian Inst. Press, Washington, D.C.

Clancey, P. A. 1989. The gender of the genus *Batis* Boie, 1833. *Bull. Brit. Orn. Cl.* 109: 122.

Collar, N. J. & Andrew, P. 1988. *Birds to Watch.* The ICBP World Checklist of Threatened Birds. ICBP Tech. Publ., No. 8.

Colston, P. R. 1981. A newly described species of *Melignomon* (Indicatoridae) from Liberia, West Africa. *Bull. Brit. Orn. Cl.* 101: 289–291.

— 1982. A new species of *Mirafra* (Alaudidae) and new races of the Somali Long-billed Lark *Mirafra somalica*, Thekla Lark *Galerida malabarica* and Malindi Pipit *Anthus melindae* from southern coastal Somalia. *Bull. Brit. Orn. Cl.* 102: 106–114.

Corbin, K. W., Livezey, B. C. & Humphrey, P. S. 1988. Genetic differentiation among steamerducks (Anatidae: *Tachyeres*): an electrophoretic analysis. *Condor* 90: 773–781.

Cox, J. B. 1989a. Notes on the affinities of Cooper's and Cox's Sandpiper. *South Austr. Orn.* 30: 169–181.

— 1989b. The story behind the naming of Cox's Sandpiper. *Australian Bird Watcher* 12: 50–57.

Davis, L. I. 1978. More African nightjars. *Pan American Studies* 1(2): 43–52.

Davis, T. J. & O'Neill, J. P. 1986. A new species of antwren (Formicariidae: *Herpsilochmus*) from Peru, with comments on the systematics of other members of the genus. *Wilson Bull.* 98: 337–352.

Diamond, J. 1991. A new species of rail from the Solomon Islands and convergent evolution of insular flightlessness. *Auk* 108: 461–470.

Dickerman, R. F., Barrowclough, G. F., Cannell, P. F., Phelps, W. H. Jr. & Willard, D. E. 1986. *Philydor hylobius* Wetmore and Phelps is a synonym of *Automolus roraimae* Hellmayr. *Auk* 103: 431–432.

Dickinson, E. C., Kennedy, R. S. & Parkes, K. C. 1991. *The Birds of the Philippines*. BOU Checklist No. 12. British Ornith. Union, Tring, U.K.

Fitzpatrick, J. W. & O'Neill, J. P. 1986. *Otus petersoni*, a new species of screech-owl from the eastern Andes, with systematic notes on *O. colombianus* and *O. ingens*. *Wilson Bull.* 98: 1–14.

— & Willard, D. E. 1990. *Cercomacra manu*, a new species of antbird from southwestern Amazonia. *Auk* 107: 239–245.

Fjeldså, J. & Barbosa, C. E. 1983. A giant hummingbird from Paramo de Chingaza, Colombia. *Wilson Bull.* 95: 661–662.

Ford, J. & Johnstone, R. E. 1983. The Rusty-tailed Flyeater, a new species from Queensland. *Western Australian Nat.* 15: 133–135.

Forshaw, J. M. 1989. *Parrots of the World*. 3rd (rev.) ed. Lansdowne Editions, Willoughby, NSW, Australia.

Fry, C. H. & Smith, D. A. 1985. A new swallow from the Red Sea. *Ibis* 127: 1–6.

Gatter, W. 1985. Ein neuer Bülbül aus Westafrika (Aves: Pycnonotidae). *Jour. f. Ornith.* 126: 155–161.

Gonzales, P. C. & Kennedy, R. S. 1990. A new species of *Stachyris* babbler (Aves: Timaliidae) from the Island of Panay, Philippines. *Wilson Bull.* 102: 367–379.

Grantsau, R. 1968. Uma nova espécie de *Phaethornis* (Aves, Trochilidae). *Pap. Avulsos, Zool., Sâo Paulo* 22: 57–59.

— 1969. Uma nova espécie de *Threnetes* (Aves, Trochilidae). *Pap. Avulsos, Zool., Sâo Paulo* 22: 245–247.

— & de Ameida Camargo, H. F. 1989. Nova espécie brasileira de Amazona (Aves: Psittacidae). *Rev. Brasil. Biol.* 49: 1017–1020.

— & — 1990. Eine neue Papageinart aus Brasilien, *Amazona kawalli* (Aves: Psittacidae). *Trochilus* 11: 103–138.

Graves, G. R. 1987. A cryptic new species of Antpitta (Formicariidae: *Grallaria*) from the Peruvian Andes. *Wilson Bull.* 99: 313–321.

— 1988. *Phylloscartes lanyoni*, a new species of bristle-tyrant (Tyrannidae) from the lower Cauca Valley of Colombia. *Wilson Bull.* 100: 529–534.

—, O'Neill, J. P. & Parker, T. A. III 1983. *Grallaricula ochraceifrons*, a new species of antpitta from northern Peru. *Wilson Bull.* 95: 1–6.

— & Weske, J. S. 1987. *Tangara phillipsi*, a new species of tanager from the Cerros del Sira, eastern Peru. *Wilson Bull.* 99: 1-6.

Hadden, D. 1983. A new species of thicket warbler *Cichlornis* (Sylviinae) from Bougainville Island, North Solomons Province, Papua New Guinea. *Bull. Brit. Orn. Cl.* 103: 22–25.

Harrison, P. 1985. *Seabirds: an Identification Guide*. Houghton Mifflin Co., Boston, Revised Edition.

Hayman, P., Marchant, J. & Prater, T. 1986. *Shorebirds, an Identification Guide to the Waders of the World*. Houghton Mifflin Co., Boston.

Hinkelman, C. 1988a. On the identity of *Phaethornis maranhaoensis* Grantsau, 1968 (Trochilidae). *Bull. Brit. Orn. Cl.* 108: 14–18.

— 1988b. Comments on recently described new species of hermit hummingbirds. *Bull. Brit. Orn. Cl.* 108: 159–169.

Humphrey, P. S. & Thompson, M. C. 1981. A new species of steamer-duck (*Tachyeres*) from Argentina. *Occ. Papers Mus. Nat. Hist. Univ. Kansas* No. 95: 1–12.

Jensen, F. P. 1983. A new species of sunbird from Tanzania. *Ibis* 125: 447–449.

— 1985. Something new under the sun. *Animal Kingdom* 88(5): 18–21.

Jouventin, P., Martinez, J. & Roux, J. -P. 1989. Breeding biology and current status of the Amsterdam Island Albatross *Diomedea amsterdamensis*. *Ibis* 131: 171–182.

König, C. 1991. Taxonomische und ökologische Untersuchungen an Kreischeulen (*Otus* spp.) des südlichen Südamerika. *Jour. f. Ornith.* 132: 209–214.

— & Straneck, R. 1989. Eine neue Eule (Aves: Strigidae) aus Nordargentinien. *Stuttgarter Beitr. z. Naturkunde*, Ser. A (Biol.), Nr. 428: 1–20.

Lanyon, S. M., Stotz, D. F. & Willard, D. E. 1990. *Clytoctantes atrogularis*, a new species of antbird from Western Brazil. *Wilson Bull.* 102: 571–580.

Lawson, W. J. 1984. The West African mainland forest dwelling population of *Batis*; a new species. *Bull. Brit. Orn. Cl.* 104: 144–146.

LeCroy, M. & Vuilleumier, F. 1990. Guidelines for the description of new species in ornithology. *Acta XX Cong. Internat. Ornith.* (Suppl.): 378. (Abstract.)

Lequette, B. & Jouventin, P. 1991. Comparison of visual and vocal signals of great albatrosses. *Ardea* 79: 383–394.

Livezey, B. C. 1986. Phylogeny and historical biogeography of steamer-ducks (Anatidae: *Tachyeres*). *Syst. Zool.* 35: 458–469.

Longmore, N. W. & Boles, W. E. 1983. Description and systematics of the Eungella Honeyeater *Meliphaga hindwoodi*, a new species of honeyeater from central eastern Queensland, Australia. *Emu* 83: 59–65.

Louette, M. 1981. A new species of honeyguide from West Africa. *Rev. Zool. Afr.* 95(1): 131–135.

— 1987. A new weaver from Uganda? *Ibis* 129: 405 – 406.

— 1990. A new species of nightjar from Zaïre. *Ibis* 132: 349–353.

— & Benson, C. W. 1982. Swamp-dwelling weavers of the *Ploceus velatus/vitellinus* complex, with the description of a new species. *Bull. Brit. Orn. Cl.* 102: 24–31.

Marshall, J. T. & King, B. F. 1988. The genus *Otus*; pp. 331–336 in *Hawks and Owls of the World*: a distributional and taxonomic list, by D. Amadon and J. Bull. *Proc. Western Found. Vert. Zool.* 3(4): 295–357.

Mayr, E. 1957. New species of birds described from 1941 to 1955. *Jour. f. Ornith.* 98: 22–35.

— 1971. New species of birds described from 1956 to 1965. *Jour. f. Ornith.* 112: 302–316.

—, Traylor, M. A. Jr. & Watson, G. E. 1986. *Check-list of Birds of the World*. Volume XI. Mus. Comp. Zool., Cambridge, Massachusetts.

— & Vuilleumier, F. 1983. New species of birds described from 1966 to 1975. *Jour. f. Ornith.* 124: 217–232.

Meise, W. 1934. Fortschritte der ornithologischen Systematik seit 1920. *Proc. VIII Cong. Internat. Ornith.*: 49–189.

— 1938. Exposition de types d'oiseaux nouvellement décrits au Muséum de Paris. *Proc. IX Cong. Internat. Ornith.*: 46–51.

Monroe, B. L., Jr. 1991. A reconsideration of the Massachusetts "Cox's Sandpiper". *American Birds* 45: 232–233.

Morony, J. J., Bock, W. J. & Farrand, J. 1975 *Reference List of the Birds of the World*. Amer. Mus. Nat. Hist., New York.

Murphy, R. C. 1936. *Oceanic Birds of South America*. Amer. Mus. Nat. Hist., New York.

Nores, M. 1986. Diez nuevas subespecies de aves provenientes de islas ecológicas argentinas. *Hornero* 12: 262–273.

— & Yzurieta, D. 1979. Una neuva especie y dos nuevas subespecies de Aves (Passeriformes). *Acad. Nac. Cienc. Cordoba Misc. no.* 61.

Olson, S. L. 1973. A classification of the Rallidae. *Wilson Bull.* 85: 381–446.

Orenstein, R. & Pratt, H. D. 1983. The relationships and evolution of the Southwest Pacific warbler genera *Vitia* and *Psamathia* (Sylviinae). *Wilson Bull.* 95: 184–198.

Parker, S. A. 1982. A new sandpiper of the genus *Calidris*. *South Australian Nat.* 56: 63.

— 1984. The extinct Kangaroo Island Emu, a hitherto-unrecognized species. *Bull. Brit. Orn. Cl.* 104: 19–22.

Parker, T. A. III & O'Neill, J. P. 1985. A new species and a new subspecies of *Thryothorus* wren from Peru. Pp. 9–15 in *Neotropical Ornithology*. Ornithol. Monogr. No. 36, P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely & F. G. Buckley eds., Amer. Ornithol. Union, Washington, D.C.

Payne, R. B. 1982. Species limits in the Indigobirds (Ploceidae, *Vidua*) of West Africa: mouth mimicry, song mimicry, and description of new species. *Misc. Publ. Mus. Zool. Univ. Michigan* No. 162: iv & 96 pp.

Pearman, M. 1990. Behaviour and vocalizations of an undescribed Canastero *Asthenes* sp. from Brazil. *Bull. Brit. Orn. Cl.* 110: 145–153.

Prigogine, A. 1978. A new ground-thrush from Africa. *Gerfaut* 68: 482–492.

— 1983. Un nouveau *Glaucidium* de l'Afrique centrale. *Rev. Zool. Afr.* 97: 886–895.

— 1985. Recently recognized bird species in the Afrotropical Region—a critical review. Pp. 91–114 in K. -L. Schuchman, ed. *Proc Intern. Symp. African Vertebrates, Zool.* Forschungsinstitut u. Mus. A. Koenig, Bonn.

— 1989. The taxonomic status of *Zoothera kibalensis*. *Gerfaut* 79: 189–190.

Rand, A. L. & Rabor, D. S. 1952. Two new birds from Philippine Islands. *Chicago Acad. Sci., Nat. Hist. Misc.* No. 100: 1–3.

Remsen, J. V. & Traylor, M. A. Jr. 1989. *An Annotated List of the Birds of Bolivia*. Buteo Books, Vermillion, South Dakota.

Ridgely, R. S. & Robbins, M. B. 1988. *Pyrrhura orcesi*, a new parakeet from southwestern Ecuador, with systematic notes on the *P. melanura* complex. *Wilson Bull.* 100: 173–182.

Ripley, S. D. 1985. Relationships of the Pacific Warbler *Cichlornis* and its allies. *Bull. Brit. Orn. Cl.* 105: 109–112.

Robson, C. R., Eames, J. C., Wolstencroft, J. A., Cu, N. & La, T. V. 1989. Recent records of birds from Viet Nam. *Forktail* 5: 71–97.

Roux, J. P., Jouventin, P., Mougin, J. L., Stahl, J. C. & Weimerskirch, H. 1983. Un nouvel albatross *Diomedea amsterdamensis* n. sp. découvert sur l'ile Amsterdam (37°50′S, 77°35′E). *L'Oiseau et R. F. O.* 53: 1–11.

Rozendaal, F. G. 1987. Description of a new species of Bush Warbler of the genus *Cettia* Bonaparte, 1834 (Aves: Sylviidae) from Yamdena, Tanimbar Islands, Indonesia. *Zool. Mededel.* 61: 177–202.

Ruschi, A. 1972. Uma nova espécie de Beija-flor do E. E. Santo. *Phaethornis margarettae*—Ruschi. *Bol. Mus. Biol. Prof. Mello Leitão*, Ser. Zool. No. 35.

— 1973a. Uma nova espécie de beija-flor do E. E. Santo. *Bol. Mus. Biol. Prof. Mello Leitâo, Santa Teresa*, Ser. Zool. *No.* 36.

— 1973b. Uma nova espécie de Threnetes (Aves. Trochilidae). *Bol. Mus. Biol. Prof. Mello Leitâo, Santa Teresa*, Ser. Zool. *No.* 37.

— 1975. *Threnetes cristinae* n. sp. *Bol. Mus. Biol. Prof. Mello Leitâo, Santa Teresa*, Ser. Zool. *No.* 38.

Ruwet, J. C. 1963. Notes écologiques et éthologiques sur les oiseaux des plaines de la Lufira supérieure (Katanga), I. *Rev. Zool. Bot. Afr.* 68: 1–60.

Salomonsen, F. 1961. A new Tit-Babbler (*Stachyris hypogrammica*, sp. nov.) from Palawan, Philippine Islands. *Dansk, Orn. For. Tidsskr.* 55: 219–221.

Schodde, R. 1982. *The Fairy Wrens, a Monograph of the Maluridae*. Lansdowne Editions, Melbourne.

— 1984. First specimens of Campbell's Fairy-wren, *Malurus campbelli*, from New Guinea. *Emu* 84: 249–250.

— 1985. The Rusty-tailed Flyeater *Gerygone ruficauda* Ford and Johnstone – a case of mistaken identity? *Emu* 85: 49–50.

— & Weatherly, R. G. 1982 [=1983]. Campbell's Fairy Wren *Malurus campbelli*, a new species from New Guinea. *Emu* 82 Supplement: 308–309.

Schulenberg, T. S., Allen, S. E., Stotz, D. F. & Wiedenfeld, D. A. 1984. Distributional records from the Cordillera Yanachaga, central Peru. *Gerfaut* 74: 57–70.

— & Binford, L. C. 1985. A new species of tanager (Emberizidae: Thraupinae, *Tangara*) from southern Peru. *Wilson Bull.* 97: 413–420.

— & Williams, M. D. 1982. A new species of antpitta (*Grallaria*) from northern Peru. *Wilson Bull.* 94: 105–113.

Sibley, C. G. & Monroe, B. L. Jr. 1990. *Distribution and Taxonomy of Birds of the World*. Yale Univ. Press, New Haven.

Stap, D. 1990. *A Parrot Without a Name. The Search for the Last Unknown Birds on Earth*. Alfred A. Knopf, New York.

Stepanyan, L. S. 1990. A new hypothesis of the origin of Cox's Sandpiper *Calidris paramelanotos* (Scolopacidae, Aves). *Zool. Zh.* 69: 148–151.

Teixeira, D. M. 1987a. A new tyrannulet (*Phylloscartes*) from northeastern Brazil. *Bull. Brit. Orn. Cl.* 107: 37–41.

— 1987b. Notas sobre *Terenura sicki* Teixeira & Gonzaga, 1983 (Aves: Formicariidae). *Bol. Mus. Paraense Emilio Goeldi*, Ser. Zool. 3: 241–251.

— & Carnevalli, N. 1989. Nova espécie de *Scytalopus* Gould, 1837, do nordeste do Brasil (Passeriformes, Rhinocryptidae). *Bol. Mus. Nac.*, Nov. Ser., Zool. No. 331: 1–11.

Teixeira, D. M. & Gonzaga, L. P. 1983a. Un novo Furnariidae do nordeste do Brasil: *Philydor novaesi* sp. nov. (Aves: Passeriformes). *Bol. Mus. Paraense Emilio Goeldi*, Nov. Ser., Zool. No. 124: 1–22.

— & — 1983b. A new antwren from northeastern Brazil. *Bull. Brit. Orn. Cl.* 103: 133–135.

—, Nacinovic, J. B. & Luigi, G. 1988. Notes on some birds of northeastern Brazil (3). *Bull. Brit. Orn. Cl.* 108: 75–79.

—, — & Pontal, F. B. 1987. Notes on some birds of northeastern Brazil (2). *Bull. Brit. Orn. Cl.* 107: 151–157.

Traylor, M. A. 1979. Subfamily Elaeniinae, pp. 3–112, *in* M. A. Traylor Jr (Ed.), *Check-list of Birds of the World.* Mus. Comp. Zool., Harvard Univ., Cambridge, Mass.

Vielliard, J. 1976. La Sitelle kabyle. *Alauda* 44: 351–352.

— 1990. Una nova espécie de *Asthenes* da serra do Cipó, Minas Gerais, Brasil. *Ararajuba* 1: 121–122.

Vo Quy 1975. *Birds of Vietnam*, Book 1. *Physical appearance and classification.* Science and Technology Publishing House, Hanoi. (In Vietnamese.)

Vuilleumier, F. 1976. La notion d'espèce en ornithologie. Pp. 29–65 *in* C. Bocquet, J. Gènermont and M. Lamotte, eds. *Les Problèms de l'Espèce dans le Règne Animal*, Tome I. Soc. Zool. de France, Mém. No. 38, Paris.

— & Mayr, E. 1987. New species of birds described from 1976 to 1980. *Jour. f. Ornith.* 128: 137–150.

Weske, J. S. & Terborgh, J. W. 1981. *Otus marshalli*, a new species of screech-owl from Peru. *Auk* 98: 1–7.

Wetherbee, D. K. 1985. The extinct Cuban and Hispaniolan macaws (*Ara*, Psittacidae), and description of a new species, *Ara cubensis. Caribbean Jour. Sci.* 21: 169–175.

Wetmore, A. & Phelps, W. H., Jr. 1956. Further additions to the list of birds of Venezuela. *Proc. Biol. Soc. Wash.* 69: 1–10.

White, C. M. N. & Bruce, M. D. 1986. *The Birds of Wallacea (Sulawesi, The Moluccas & Lesser Sunda Islands, Indonesia).* B.O.U. Checklist No. 7, British Ornithologists' Union, London.

Wiedenfeld, D. A. 1982. A nest of the Pale-billed Antpitta (*Grallaria carrikeri*) with comparative remarks on antpitta nests. *Wilson Bull.* 94: 580–582.

Yamashina, Y. & Mano, T. 1981. A new species of rail from Okinawa Island. *Jour. Yamashina Inst. Ornith.* 13: 1–6.

Zimmer, J. T. & Mayr, E. 1943. New species of birds described from 1938 to 1941. *Auk* 60: 249–262.

Addresses: François Vuilleumier and Mary LeCroy, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA; Ernst Mayr, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, USA.

© British Ornithologists' Club 1992

EPILOGUE

One hundred years on, the founding fathers of the British Ornithologists' Club would be daunted indeed by today's systematics and its specialised techniques. They would, too, be dismayed at the disregard amounting to disdain of trustees and managers of the great natural history museums of Europe for orthodox museum work and research. They would approve greatly of modern sophisticated field identification and methods, and the undreamed of optical and sound-recording facilities by which they prosper, even maybe to the extent of dismissing their doubts on the admissibility of sight records. They would be equally astonished at what they would deem the mistaken sentimentality towards collecting specimens for museum work, to them the heart of taxonomy and systematics – as indeed it is to the diminishing band of museum based workers still pursuing their calling today.

Taxonomy being essentially based on skill and experience in making comparisons between closely similar or unlike or totally dissimilar specimens, if species and subspecies are to remain the foundation building blocks of systematics, it is hard to see how an unambigously designated type specimen – in birds, in the form of the conventional museum 'skin' – can be dispensed with. Relationships beween families and genera may well in due course become convincingly determined by ever increasingly sophisticated methods of assaying hereditary characters; but will the subjectivity involved in measuring and judging the degree of difference between museum specimens become a thing of the past, substituted perhaps by drops of blood or by frozen tissue? Plainly that time has not yet come.

This volume draws attention to and emphasises the importance of avian systematics and taxonomy, so long a leader in advancing theories in the wider field of evolution. It is manifestly an active science, not merely in its own at present somewhat disparaged field, but also in its academic role and the application of its expertise for the better understanding of problems in other zoological disciplines. It is to be hoped that fresh thinking by the proponents of present day museum management may yet revert to encouraging the creative use of the historic collections in their care, which originated with the immediate forefathers of the founders of the British Ornithologists' Club.

JAMES MONK

Goring-on-Thames
Oxfordshire

© British Ornithologists' Club 1992

CONTENTS

Page

PREFACE ERNST MAYR 1

BOCK, W. J. Status and future activities of the Standing Committee on Ornithological Nomenclature of the International Ornithological Committee (IOC) 3

AMADON, D. & SHORT, L. L. Taxonomy of lower categories—suggested guidelines 11

BARROWCLOUGH, G. F. Biochemical studies of the higher level systematics of birds 39

BOCK, W. J. Methodology in avian macrosystematics 53

CLANCEY, P. A. Subspeciation, clines and contact zones in the southern Afrotropical avifauna 73

FRY, C. H. Myrmecophagy by *Pseudochelidon eurystomina* and other African birds 87

GRANT, P. R. Systematics and micro-evolution 97

HAFFER, J. The history of species concepts and species limits in ornithology 107

JACOB, J. Systematics and the analysis of integumental lipids: the uropygial gland 159

KNOX, A. G. & WALTERS, M. Under the skin: the bird collections of the Natural History Museum 169

LECROY, M. & VUILLEUMIER, F. Guidelines for the description of new species in ornithology 191

LÖHRL, H. & THALER, E. Behavioural traits as an aid to solving taxonomic problems 199

LOUETTE, M. Barriers, contact zones and subspeciation in central equatorial Africa 209

MOREL, G. J. & CHAPPUIS, C. Past and future taxonomic research in West Africa 217

OUELLET, H. Speciation, zoogeography and taxonomic problems in the Neotropical genus *Sporophila* (Aves: Emberizinae) 225

PANOV, E. N. Emergence of hybridogenous polymorphism in the *Oenanthe picata* complex 237

POTAPOV, R. L. Systematic position and taxonomic level of grouse in the order Galliformes 251

VOOUS, K. H. Reflections on the genus in ornithology 261

VUILLEUMIER, F., LECROY, M. & MAYR, E. New species of birds described from 1981 to 1990 267

MONK, J. F. Epilogue 311

Published by the BRITISH ORNITHOLOGISTS' CLUB and printed by
Henry Ling Ltd., at the Dorset Press, Dorchester, Dorset